Plant Species and Functional Diversity along Altitudinal Gradients, Southwest Ethiopian Highlands

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Summary

Understanding how biodiversity is organized across space and time has long been a central focus of ecologists and biogeographers. Altitudinal patterns of richness gradients are one of such striking patterns in the landscape. Despite its historical and ecological importance as a heuristic natural experimental site for development of ecological theories, the emergent patterns and mechanisms that structure them are poorly understood. This is partly because of the complex relationships of species to the environment and the choice of the response variable itself, i.e. using taxonomic richness as a metrics of diversity. This thesis, therefore, applies plant functional types (hereafter PFTs) approach to study the response of vegetation to environmental factors in the southwest Ethiopian highlands. It focuses on the classification of the vegetation into a few main plant functional response categories and relate them to environmental variables. For pattern identification and mechanistic explanations, a deconstructive approach of the taxonomic richness into its constituent components was used. Furthermore, the potential effects of land use/land cover change and global warming on the biodiversity of the study area was investigated.

The results reveal that the application of plant functional types is a promising tool to understand vegetation-environment relationships. Local topographic attributes (altitude and slope) and soil properties found to structure the variance in the relative abundance of PFTs along environmental gradients. Moreover, specific response to drought favours the abundance of species with thorns/spines and tussocks in the lowlands as opposed to chilling which favours rosettes and rhizomes PFTs in the highlands. Concerning patterns of richness along altitudinal gradients, various structures of richness appear for total vascular plant species and growth forms. Woody plants, graminoids and climbers showed a uni-modal structure while ferns and herbs revealed an increasing pattern of richness along the altitudinal gradient. By contrast, total vascular plants species richness did not show any strong response to altitudinal gradients. Climate related water-energy dynamics, species area relationships due to the physical shape of the mountain, local topographic and soil conditions were found to be predominant factors structuring the observed richness in the study area.

The threats to biodiversity loss due to land use/land cover change and global warming is eminent in the study area. Land conversion for agricultural purposes was a pervasive process that had a deleterious effect on the biodiversity of the study area. Population growth, socio-

economic challenges (poverty) and government policy regimes drive land cover change processes. In addition, recent climate change poses a serious challenge to the biodiversity of the study area. The results of model predictions indicated that biodiversity of the study area will suffer severe consequences of lowland biotic attrition (i.e. the net loss of species richness in the tropical lowlands caused by altitudinal range shifts in the absence of new species arriving), range gap shifts and contraction, and extinction due to expected warming at the end of this century. The model also predicted that endangered and endemic species with restricted elevational ranges will disproportionately suffer from range contraction and extinction due to warming.

In conclusion, the plant functional types approach was found to be an essential tool to reduce complexity of the vegetation of the study system and to elucidate vegetation-environment relationships. Moreover, the identification of emergent patterns and attributing them to mechanistic explanations are pre-requisites for conservation planning to save biodiversity of the study area. The study also evidenced that land use/land cover change and global warming will present strong threats to the loss of biodiversity in the study area. Salvaging biodiversity in the future requires the consideration of the effect of land use and climate change on vegetation responses. Consequently, nature conservation strategies and future reserve designs should take into account options of human assisted migration across fragmented landscapes and creating dispersal routes for species to track to new thermal niches.

Zusammenfassung

Seit längerem streben Biogeographen und Ökologen nach dem Verständnis, wie Biodiversität in Zeit und Raum organisiert ist. Die höhenbedingte Abnahme der Vielfalt ist hierbei eines der prägenden Landschaftsbilder. Trotz der historisch gewachsenen ökologischen Bedeutung als heuristisches, natürliches Studiengebiet sind die zugrundeliegenden Muster und Mechanismen noch weitgehend unklar. Dies liegt nicht zuletzt an der komplexen Beziehung zwischen Arten zu ihrer Umwelt und auch in der Wahl der Untersuchungsmethodik an sich. Als Beispiel sei der häufige Gebrauch der taxonomischen Vielfalt als ausschließliches Biodiversitätsmaß genannt.

Diese Arbeit wendet insofern den erweiterten Ansatz der Pflanzenfunktionstypen an (im Folgenden: PFTs) um die Reaktion der Vegetation auf diverse Umweltfaktoren im Südwesten des äthiopischen Hochlandes zu erforschen. Ziel der Studie ist es, die Vegetation in einige wenige Hauptkategorien von Pflanzenfunktionstypen zu klassifizieren und diese in Bezug zu ihrer Reaktion auf Umweltvariablen zu setzen. Der Ansatz der taxonomischen Vielfalt wurde somit und ergänzt, um sowohl räumliche Muster zu identifizieren, als auch die dahinter befindlichen Mechanismen erklären zu können. Darüber hinaus wurden sowohl potentielle Einflüsse von Landnutzungs- und Landbedeckungswandel, als auch die Auswirkungen der globalen Erwärmung auf die Biodiversität des Untersuchungsgebietes analysiert.

Die Ergebnisse verdeutlichen, dass der Ansatz von Pflanzenfunktionstypen vielversprechend ist, um Vegetation-Umwelt-Beziehungen zu verstehen. Lokale topographische Parameter (z.B. Höhe und Hangneigung) scheinen die Varianz in der relativen Häufigkeit der PFTs entlang eines Umweltgradienten zu beeinflussen. Des Weiteren erklärt die spezifische Adaption an Hitzeereignisse die hohe Abundanz von Arten mit Dornen/Stacheln und Tussock-Gras in den niederen Lagen.

Hinsichtlich der Vielzahl von Arten entlang des Höhengradientens, scheinen verschiedene Strukturmuster für die Gesamtheit der Gefäßpflanzen und Wuchsformen zu existieren. Holzgewächse, Schlingpflanzen und Graminoide kennzeichnet eine Verteilung entlang der Höhe, wohingegen Farne und Krautartige entlang des Höhengradientens in ihrer Häufigkeit zunehmen. Demgegenüber besteht nur ein schwacher Zusammenhang zwischen der Gesamtzahl an Gefäßpflanzen und der Höhe. Im Untersuchungsgebiet wurde die

klimabedingte Wasser-Energiedynamik, das Arten-Flächenverhältnis in Bezug zum Gebirgsprofil, lokale topographische Einflüsse sowie Bodencharakteristika als entscheidende Einflussgrößen hinsichtlich der beobachteten Vielfalt erkannt.

Introduction

Drivers of Diversity Patterns

Diversity is unevenly distributed over the surface of the earth. The most conspicuous spatial pattern of species diversity is a latitudinal gradient of decreasing richness of species from equator to poles (Gaston 2000; Willig *et al.* 2003). This pattern is consistent for several organismal groups such as terrestrial plants (Mutke & Barthlott 2005; Barthlott *et al.* 2007), coral reefs, mammals, fish and birds (Willig *et al.* 2003). However, notable exceptions to this classical pattern are quite common for different taxonomic groups (Heywood 1995). Some taxonomic groups such as vascular plants richness in Africa increases towards temperate latitudes (Heywood 1995), hotspots of gymnosperm diversity are located in Southeast Asia especially in China while tropical Africa is considered as a cold spot of Gymnosperm species diversity (Mutke & Barthlott 2005).

Another striking pattern of species diversity is an altitudinal diversity gradient (Lomolino 2001). The elevational clines on species diversity were one of the central themes to explain the origin and diversification of biota (von Linnaeus 1743) and identified as one of the most important biogeographic patterns by early naturalists (von Humboldt 1849), and an important experimental site for the development of contemporary ecological theories (Whittaker 1960; Brown 1971; Whittaker 1972). Generally, species diversity tends to decrease with altitude (Rahbek 1995; Brown & Lomolino 1998). As such, species richness pattern along altitudinal gradients was simply compared to the latitudinal gradients (Brown & Lomolino 1998; Lomolino 2001). Nevertheless, several studies have documented a non-monotonic pattern of species richness (Rahbek 1995; Bhattarai & Vetaas 2003). The most commonly observed pattern of diversity is a mid-altitudinal bulge (Rahbek 2005). There is also evidence of a mid-altitudinal trough in species richness gradients along altitude (Peet 1978).

Obviously these observed patterns at different spatial scales required mechanistic explanations. The attempts to account for such explanations have taken mainly in two directions: the deterministic aspect of the physical environment and historical-evolutionary processes (Brown & Lomolino 1998; Gaston 2000; Ricklefs 2006). The former considers variations in the physical environment as the primary determinants of species diversity across spatial scales (Willig *et al.* 2003). The general notion here is that variations in the number of

species is an outcome of species interactions at particular environmental settings (Ricklefs 2006). Thus, the biological processes (e.g competition, predation) are inherently thought to be guided by particular environmental settings and play a role to determine the species diversity of a community in a region of interest.

The latter refers to the importance of history and evolutionary mechanisms such as speciation and extinction as stochastic processes to create and maintain diversity. Historical and evolutionary process is believed to play an important role in large scale patterns of diversity (Whittaker 2004) but also controls external drivers for local diversity (e.g. regional pool of species from which the environment can filter) (Keddy 1992). However, recently there is a consensus that both processes work in tandem to structure diversity at different spatial scales, albeit, the relative importance of one over the other is still dependent on the scale of observation (Whittaker 2004).

Processes driving global scale diversity patterns could be a result of evolutionary processes, interacting with large scale and long term climatic conditions (Willis & Whittaker 2002; Whittaker 2004). In regard to latitudinal variation in species diversity, a number of hypotheses were forwarded such as energy availability, water-energy dynamics, environmental stability, habitat heterogeneity, species-area relationship, Rapoport´s rule (species range size), and time (Gaston 2000). Nonetheless each of these could lend only a part when explaining the gradient in diversity from tropics to temperate latitudes. Yet, the general consensus is that the tropics had a constantly high environmental temperature compared to temperate regions and a long evolutionary time was available for species to accumulate (Willig *et al.* 2003; Kreft & Jetz 2007). These two factors together or independently may have led to the accumulation of species, niche specialization and other biological processes to generate higher species diversity in the tropics compared to temperate latitudes, which had observed different cycles of climatic oscillations and shorter time for accumulation of species (Brown & Lomolino 1998).

Apparently, high diversity of species in the tropics is sustained by relatively infertile and nutrient poor soils. The tropical soils are characterized by nutrient depletion since the soils are formed from old continental shields (e.g. in Africa) and has not been rejuvenated by oceanic sediment deposition since the late Mesozoic era (Breckle 2002). In addition, because of high rainfall (and temperature) in the tropics soils were exposed to heavy leaching (Walter 1985).

Thus, most of the soils are nutrient deficient in the essential soluble minerals required by plants such as phosphorous. The fact that Ethiopia is located in the tropics has a constant environmental temperature and a long time of ecosystem development, which favoured ecological and evolutionary processes to generate high species diversity and endemism (Umer *et al.* 2007).

Unlike the general picture of the tropics, however, Ethiopia is characterized by a complex geological history. The tertiary build-up of trappean series volcanic mountains and subsequent rifting created complex heterogeneous landscapes in the country. Thus, the Ethiopian highlands and Rift Valley systems alike have been, and continue to be, rejuvenated by essential plant nutrients through weathering processes. In addition, the formation of the highland systems provided wide ranges of environmental templates along altitudinal gradients for species to shift up and down during past climate changes (Bobe 2006).

Other peculiar characteristics of the study area are that it is the only part in the world where semi-arid ecosystems are developed without the direct influence of rain-shadow effect (e.g. South American semiarid environments) (Roig-Junent *et al.* 2006), continental interior (e.g. Mongolia, South Central North America) and cool ocean currents in the parts of Namibia and South Africa, Western Australia (Martin 2006). However the emergence of semiarid ecosystem in East Africa is related to interaction of multiple environmental and biogenic factors (Bobe & Behrensmeyer 2004; Bobe 2006). Generally in Africa in the early Mesozoic (65 Ma) large scale extinction of mega-herbivores occurred. The extinction of these mega-herbivores promoted the development of woody and closed vegetation as the grazing, browsing and devouring effects of animals declined (Bobe 2006).

During the Eocene declining global temperature and concomitant decline in precipitation, however, resulted in the emergence of open habitats and arid adapted vegetation (Bobe & Behrensmeyer 2004). Evidence from carbon isotope indicated that expansion of C_4 grass vegetation at about 1.8 Ma in east Africa (Cerling 1992) and hence most parts of east Africa was dominated by C_4 grasses in the Pleistocene period (Bobe & Behrensmeyer 2004). Thus, these shifts in ecosystem from C_3 dominated vegetation, mostly trees and shrubs, to C_4 vegetation, mainly dominated by grasses, have added complexity in environmental heterogeneity. Consequently, the environmental history of Africa was characterized by multiple changes, and a complex interactions of climatic, tectonic (e.g. rift valley formations),

and biotic factors (browsing and grazing dynamics), and often fire and land use history since the late stone age (Potts 1994; Bobe 2006).

Concerning the mechanisms explaining altitudinal gradients of diversity, there were a number of factors considered to be important for elevational clines of diversity (Lomolino 2001). Some of these may include climatic factors mainly rainfall and temperature, area effect, and increased isolation with elevation (Brown & Lomolino 1998). In regard to climatic factors, mainly temperature and rainfall, temperature decreases with increasing altitude while rainfall increases non-linearly with altitude in the tropics and hence produce a double complex gradient and affect the abundance and diversity of species along the mid altitudinal gradient (Brown & Lomolino 1998).

The other factor, which was thought to affect the pattern of species diversity along altitudinal gradient, is the effect of area. As altitude increases the total area decreases towards the top of a mountain (Körner 2000). This small area effect with increasing isolation of habitats at higher altitudes would result in lower number of species at the upper end of the gradient (Lomolino 2001). As tops of mountains tend to be isolated, it is highly probable that species dispersal and exchange events will be lower there (Brown & Lomolino 1998; Lomolino 2001).

Topographic and other environmental heterogeneity gains more importance in explaining the variation in species diversity at landscape scales (O'Brien *et al.* 2000). Heterogeneity is an indicator of the resource availability variation in spatiotemporal contexts, there by generating the possibility of niche partitioning among organisms. Environmental heterogeneity of a site in the landscape is generally related to the variation in relief, bedrock and edaphic conditions, and disturbance at different spatial and temporal scales (Huston 1994). Topographic heterogeneity owing to the effect of slope, aspect and altitude affects the distribution of individual plants and communities by indirectly regulating the distribution of moisture, nutrients and through the influence of micro-climatic and hydrological processes in the site (Parker & Bendix 1996).

Similarly, substrate heterogeneity as a result of the variation in the soil texture and nutrient availability, which are mainly the result of geological processes, influences patterns of species diversity distributions (Huston 1994). This thesis focuses on the predominant environmental

determinants of species diversity at the landscape level such as variations in altitude, soils and topography (see also Whittaker 2004). However, the historical and evolutionary context (e.g. climate history, tertiary orogenic episoides, evolutionary time), which is believed to affect the diversity pattern at broader regional scales (Willig *et al.* 2003; Whittaker 2004; Kreft & Jetz 2007), sets a background condition to the subsequent lower level diversity patterns (Ricklefs 2006).

Deconstruction of Diversity Patterns

The concept of biological diversity incorporates "the variability among living organisms from all sources ranging from genetic to ecological complexes in which they are part" (Houston 1994; Heywood 1995; Roy *et al.* 2004). The taxonomic (species) richness, based on Linnaeus binomial classification, is generally used as a common currency to measure the overall variability of life on earth. Moreover, species richness has invariably been used to investigate the response and effects of biodiversity on ecosystems. However, some authors (e.g. Hooper *et al.* 2002) argued that species richness lacks the explicit power to explain ecosystem level processes, stressing that the functional attributes of species may constitute a better approach to relating global environmental change and inherent ecosystem processes than taxonomic richness. Therefore, other aspects of diversity (e.g. morphological or functional) have started to gain importance in the last few decades (Cody 1991; Marquet *et al.* 2004; Roy *et al.* 2004).

Patterns of diversity vary when species richness is disaggregated into different components (Bhattarai & Vetaas 2003; Marquet *et al.* 2004). Hence, plant functional classification has been used as an essential tool to reduce the floristic complexity of vegetation (e.g. Lavorel *et al*. 2007). This classification attempts help to investigate mechanisms that structure the patterns of diversity (Marquet *et al.* 2004; Roy *et al.* 2004), to investigate response of vegetation to environmental gradients and disturbance (Diaz *et al.* 1999), and to relate attributes of species to ecosystem properties (Diaz & Cabido 1997). The fact that vascular plants adapt morphologically to various environmental factors such as water supply, temperature, and light environments, a deconstruction of the richness components of diversity into different functional/morphological categories will decipher a better picture of diversity patterns in the landscape (see **Manuscript 1**).

Plant functional types are defined as sets of species that demonstrate either a similar response to the environment or have similar effects on major ecosystem processes (Gitay & Noble

1997). PFTs are grouped according to their morphological, physiological, regenerative or phenological features (Lavorel & Garnier 2002), rather than their phylogenetic relationships. This provides the opportunity to directly link functional response traits with environmental variables such as climate, disturbance regimes, and resource availability (Hooper *et al.* 2002). The term functional diversity refers to the kind, range and relative abundance of functional traits, and hence PFTs, present in a given community (de Bello *et al.* 2006; Lavorel *et al.* 2007).

The variation in the relative abundance of certain plant functional types in a given landscape informs us about the strength of the dominant environmental constraint (e.g. climate, resource availability or disturbance) in that system (Keddy 1992). Consequently, plant traits which will provide competitive advantages over the others to survive under such limiting conditions will be selected. For instance, Diaz *et al*. (1999) reported the strongest climatic filtering effects of vegetative traits such as plant height, life history, carbon allocation for support or storage in central-western Argentina. The distinction between evergreen and deciduous woody species constitutes how vegetation responds to climatic rhythms (Bonan 2008) and responses to herbivory (Ganqa & Scogings 2007). Concerning climatic rhythms deciduous species shed leaves in periods of water stress or cold temperature while evergreen species grow more or less constantly and develop resistance to climatic fluctuations. Leaf phenology by woody species can also be used as a strategy to resist or avoid herbivory (see **Manuscript 2** for classification of PFTs and discussions related to the study system). Generally, evergreen species contains low leaf nitrogen (Ganqa & Scogings 2007) and invest more carbon on physical or chemical protective mechanism against herbivory than deciduous species (Bonan 2008).

Threats of Biodiversity Loss in the Tropics

In the preceding sections brief accounts were provided to discuss on the components of diversity, diversity patterns and mechanisms that generate diversity. In the following paragraphs I briefly discuss on the two major factors which contribute to the loss of biodiversity in the tropics: land use/cover change and climate change.

Land use/land cover change: Land use change has been identified as one of the most important drivers of biodiversity loss for tropical ecosystems (Sala *et al.* 2000). Land use changes are modifying and fragmenting habitats, increasing the vulnerability of ecosystems to

invasive species and have persistent legacies in shaping and maintaining ecosystem structures and functions (Foster *et al*., 2003). Habitat loss and fragmentation are decreasing suitable habitats of species and thereby forcing species extinctions (Thomas *et al.* 2004).

Regional difference in the rate of land use/land cover changes are pervasive and tropical ecosystems are particularly facing extreme levels of land cover conversions and hence an over average loss of biodiversity (Chapin III *et al.* 2001; Bradshaw *et al.* 2009). The mountain regions in the tropics are store houses of biodiversity because of their wide range of environmental templates along gradients and historical-biogeograpic importance as refugia during Pleistocene environmental changes (Messerli & Ives 1997; Bobe 2006). As such they host significant proportions of biodiversity and endemism (Burgess *et al.* 2007a; Burgess *et al.* 2007b; Umer *et al.* 2007) but at the same time were favoured by human habitation (Meyers *et al.* 2000) due to high thermal stress and tropical diseases in the low-lying areas in the tropics.

The Ethiopian highlands contain a rich floral and high level of endemism (Hedberg & Edwards 1989; Vivero *et al.* 2006). However, deforestation and land conversion for agriculture, grazing, and demand for household energy have decimated the vegetation cover of the country (Eckholm 1975; Getahun 1984; Ezra 2001). Growth in human population density and rural poverty further reinforced the process of biodiversity loss via land conversion and increased demand for household energy (McCann 1995; Gessesse & Christiansson 2008). Nevertheless, recent studies have indicated that the lowlands and the Rift Valley, which were previously less populated, are facing increasing level of land cover change (**Manuscript 3**) and consequently facing biodiversity loss due to in-migration of population from the adjacent highlands, climate change and socio-political dynamics (Reid *et al.* 2000; Spottiswoode *et al.* 2009).

Global warming and vegetation response: The earth has evidenced during the last three decades a considerable warming (Thomas *et al.* 2004; Aerts *et al.* 2006). It has been reported that global temperature has increased during this time approximately by about 0.5 °C (IPCC 2007). Global average temperature increase will inform little about the response of vegetation to global warming, rather vegetation response to specific regional temperature increase is important (Peters 1991; Aerts *et al.* 2006). Moreover, the extreme weather episodes such as drought, cold spells, flooding, etc., may have more effects on species distribution and

performance of species (Peters 1991; Jentsch *et al.* 2007). Regional models predict that temperature increase will be relatively higher for northern latitudes and mountain regions (IPCC 2007). The regional models also predicted high variability of precipitation for East Africa but a trend of increasing precipitation at the end of 21st Century (IPCC 2007). Thus, the effects of increased temperature and precipitation variability will negatively affect the biodiversity of mountain regions of East Africa because of the limited possibilities of isolated populations to move upwards (Case 2006)

Species respond to global warming by a number of ways such as *in situ* persistence and adaptations, migration and extinction (Peters 1991; Midgley *et al.* 2007). *In situ* persistence is performed through species tolerance of the vegetative stages, and longevity and dormancy of the propagules while *in situ* adaptation requires genetic variation and plasticity to adapt to a wide range of climatic stresses (Midgley *et al.* 2007). However, there is a general consensus that the earth is warming much faster than many species could adjust by *in situ* persistence and adaptations, leaving the obvious options for species to confront climate change via either migration and hence eventually tracking suitable environments for colonization or may be subjected to unprecedented level of extinction (Thomas *et al.* 2004; Midgley *et al.* 2007).

Tropical mountain ecosystems are expected to suffer disproportionately to the effects of climate change (Raxworthy *et al.* 2008; Bradshaw *et al.* 2009). Species extinction will be higher in mountain regions because of the concentration of habitat specific endemic species at the top of high mountains with restricted climate ranges and forced to shift up-wards (IPCC 2007; Raxworthy *et al.* 2008). Apart from the threat of extinctions, Colwell *et al.* (2008) have identified another three major potential ecological consequences which tropical mountain ecosystem will be expected to suffer. According to their model lowland biotic attrition, range shift gaps, and range contraction are pervasive challenges. This model has been applied to predict species and plant functional groups potential response to changes in isotherms along an altitudinal gradient (**Manuscript 4**).

Objectives, Research Questions and Hypotheses

The over all motivation of this thesis can be clustered into two main issues: (1) identifying the emergent patterns of diversity and mechanisms generating diversity in the landscape scale and (2) investigating major threats of biodiversity in the study area. Regarding the former, total

vascular plants and growth forms were modelled to predict patterns of richness and plant functional types approach was employed as a response variable to evaluate the relative abundance of plant functional types along altitudinal gradients. The latter focuses on two major factors such as land use/land cover change and climate change as drivers of biodiversity loss in the study area.

The diversity in growth forms in a given ecosystem is linked to the structural complexity and resource partitioning in the system (Cody 1991). The simple distinction of growth forms such as woody (trees and shrubs), herbs, climbers, graminoids, etc informs us about the specific adaptations to environmental conditions such climate and wind (Rowe & Speck 2005), solar energy partitioning (e.g sensible vs. latent heat) (Baldocchi *et al.* 2004) and water use efficiency in the ecosystem (Breshears & Barnes 1999). However, studies regarding patterns of growth form diversity along environmental gradients were relatively a recent phenomenon (Roy *et al.* 2004). Patterns of diversity may vary when species diversity is disaggregated into respective growth forms (Marquet *et al.* 2004) and mechanisms that generate diversity vary accordingly. This is clearly important when we consider the effect of altitude on the pattern of species diversity. We posed certain questions in this regard: Do various growth forms and total vascular plant richness follow similar patterns along the altitudinal gradient? What are the driving mechanisms that structure patterns of richness along the altitudinal gradient in the investigation area (**Manuscript 1**)?

I was also interested to classify the vegetation of the study area into a few plant functional types based on certain morphological and functional features of species (**Manuscript 2**). In the last two decades PFTs approach was applied to model the effect of global environmental change on the vegetation dynamics (Condit *et al.* 1996; Leemans 1997) and to relate plant functional traits to ecosytme functions (Diaz & Cabido 1997; Lavorel *et al.* 2007).

Most of the traits that were used for the classification of functional types were “soft traits”, which are relatively easy and quick to quantify (Cornelissen *et al.* 2003). These soft traits such as plant growth forms, spinescence (thorns/spines), specific leaf area, leaf phenology, etc., can be directly linked to certain ecological responses and processes (e.g. light interceptions, defence against herbivory, photosynthetic efficiency, nutrient resident time) (Lavorel & Garnier 2002; Cornelissen *et al.* 2003). Though there is a growing consensus among ecologists and environmental scientists to integrate plant functional types approach to

study the vegetation-environment relationships and ecosystem functions, very few research have been conducted in the African vegetation (Skarpe 1996). Most of the studies were conducted in temperate ecosystems (Diaz & Cabido 1997; de Bello *et al.* 2006; Diaz *et al.* 2007) and in the neo-tropics (Condit *et al.* 1996; Kraft *et al.* 2008). I have not come across with any literature which explicitly addressed the use of plant functional types response and effects on ecosystem processes in the Ethiopian vegetation. Nevertheless the existing studies, mainly based on floristic composition, indicate that pattern of vegetation and floristic diversity are generally governed by elevation, moisture availability, nutrient and topographic variables (Zerihun *et al.* 1989; Friis 1992; Tamrat 1994; Teshome *et al.* 2004).

The purpose of **Manuscript 2** was to find out which environmental factors set constraints to control the relative abundance of plant functional types along altitudinal gradients. Specifically, the following hypotheses were proposed: 1) Altitude and slope have a significant effect on the variation of the relative abundance of plant functional types in the study area; 2) Soil texture and fertility have a strong explanatory power to the variation in the relative abundance of plant functional types along altitudinal gradients; 3) PFTs response to stress (drought and chilling) and thus grazing would favour the abundance of distinct plant functional types such as thorny plants and tussocks in the lowlands vs. rosettes and rhizomes at higher altitudes.

The challenge of biodiversity loss is one of the big problems of modern society. A number of factors have been identified as the drivers of biodiversity loss (Ehrlich & Pringle 2008). The two prominent factors for tropical biodiversity loss are land use/land cover change and climate change (Sala *et al.* 2000). The purpose of **Manuscript 3** was to address the dynamics of land use/land cover change and its potential consequence on biodiversity. The main questions were: What are the rates and magnitudes of land use/land cover change in the study area? Do highland and Rift Valley sections of the study area show differential trajectories of land use/land cover change? What are the main driving forces for land use/land cover change in the study area?

Concerning climate change, particularly global warming, as drivers of biodiversity loss **Manuscript 4** modelled the potential ecological consequences of species in the study area. The model developed by Colwell *et al.* (2008) was applied on a dataset of altitudinal vegetation surveys in our study area. The purpose of the study was to test the following

hypotheses: 1) Consequences of global warming result in strong potential lowland attrition, range-gaps, range contractions, and finally extinction risks of plant species of southern Ethiopia. 2) There are growth forms and plant families which face a higher than average risk due to their current altitudinal distribution. 3) Endangered and endemic species are especially vulnerable to warming.

Synopsis

Thesis Outline

The thesis contains four manuscripts. It is organized along with two main issues addressed in the thesis. The first issue is on the emergent patterns of diversity and mechanisms generating diversity at the landscape scale (**Manuscripts 1 & 2**) while the second issue focuses on drivers of biodiversity loss (**Manuscripts 3 & 4**). A brief outline of each of the manuscripts is provided in the subsequent paragraphs.

Manuscript 1 deals with the issue of deconstructing richness components to its constituent parts and evaluates the pattern of richness distribution along environmental gradients. It gives special attention to growth form plant functional types because this defines the physiognomy and structure of the vegetation in the landscape. Boosted regression tree analysis was applied to predict the pattern of species and growth form richness along altitudinal gradients. The results revealed that patterns of diversity distribution would vary along altitude when the total vascular plants are disaggregated into several growth form categories. However, a hump-shaped uni-modal richness pattern was observed for woody, graminoids and climbers plant functional types. A mid-altitudinal richness peak was the result of the combination of climate related water energy-dynamics, species area-relationships and local environmental factors, which have direct effects on plants physiological performance. However, altitude represents the composite gradient of several environmental variables that are interrelated. Thus, considering multiple gradients would help to reveal a better picture of richness and the potential mechanisms that structure the distributions of biodiversity in high mountain regions of the tropics.

Manuscript 2 focuses on the response of the relative abundance of plant functional types to environmental gradients. Plant functional types were categorized into four major groups based on their expected response and adaptation to environmental variables and competition,

stress/grazing and temporal attributes. After such a classification, it evaluates the distribution of relative abundance of plant functional types along environmental gradients using constrained linear ordination techniques (RDA). The results of linear ordination analysis showed that topographic attributes such as altitude and slope, and soil organic carbon were found to be the most important factors explaining the variance in the distribution of the relative abundance of plant functional types along environmental gradients. Moreover, vegetation response to drought and grazing tends to favour the abundance of thorns/spine and tussocks plant functional types in low lands. The response to chilling and grazing favours the abundance of rosettes and rhizomatous PFTs in the highlands. This preliminary classification of the vegetation into different PFTs response categories proves to be important to understand the pattern of abundance distributions and the response to various environmental factors.

Manuscript 3 deals with the dynamics of land use/land cover changes and its anticipated consequences on the biodiversity of the study area. Time series land use/land cover classification was carried out based on ERDAS Imagine 8.5 using maximum likelihood classification techniques for the years 1976, 1986 and 2000. This provides the rate and magnitude of land use/land cover change, and discusses the main driving socio-economic processes during the specified time. The findings suggest that land use/land cover change took differential trajectories across space and time. The highlands of Gughe-Amaro Mountains were predominantly affected by land conversion to agricultural purposes. Whereas the Rift Valley section showed a combination of land use changes to cropland and class-to-class shifts (transitions) of land cover types. Temporally, after mid-1980s land cover change to cropland was predominant both in the highlands and the Rift Valley sections of the study area. The observed change in the land use/land cover was driven due to increasing population pressure, socio-economic problems (poverty) and government policy regimes. The spatial and temporal changes of the land use/land cover in the study area will have potential consequences on local human livelihoods, biodiversity loss and regional environmental change.

Manuscript 4 evaluates the potential impact of global warming on the biodiversity of the study area. We have applied a simple model developed by Colwell *et al.* (2008) regarding the potential response of tropical species to projected global warming scenarios. The Intergovernmental Panel of Climate Change (IPCC 2007) projects 4.2 ° C warming of temperature for East Africa at the end of 2100. For the prediction of potential species response to global warming we considered a range of 0 - 5° C warming scenarios (based on

A2 emission scenario) and the current atmospheric lapse rate of 0.6° C/100 m (Peyron *et al.* 2000). The results showed that lowland biotic attrition occurred with mild level of projected temperature change. However, range contraction and mountain top extinctions become apparent when temperature increases above 3.5 °C. Moreover, various growth forms have shown differential responses to warming scenarios. The model also predicted high level of vulnerability of threatened and endemic species to extinctions and range contractions due to global warming. Finally, the manuscript suggests biodiversity conservation efforts and future reserve designs should consiser the potential effect of global warming on biodiversity.

Synthesis and Conclusions

Deconstruction of diversity components: Much of the discussions on the pattern of richness along altitudinal gradients rely on the total number of species present in a given sampling effort. In this case all vascular plants are assumed to be equal or ecological equivalent and then related to the external environmental factor (Marquet *et al.* 2004). The resultant response (pattern of richness) is therefore considered as an outcome of interaction of species to the external environmental factors. This has constrained the progress to understand the underlying mechanisms that structure richness pattern. Thus part of the solution would lie on the handling of the response variable itself.

The basic rational behind disaggregating richness is that all species are not equal in their response to external environmental factors (Roy *et al.* 2004). Species can be grouped into more homogenous groups based on their morphological or functional attributes. This "reductionist approach" will reduce the floristic complexity and help to test hypothesis regarding pattern of richness along altitudinal gradients. The results of **Manuscript 1** support this notion where the pattern of richness varied with growth forms where as no strong response to total vascular plant richness. A uni-modal pattern of richness was observed for woody, graminoids and climbers while ferns and herbaceous species showed an increase with altitude. There was also variation among growth forms which showed uni-modal structure: the richness of graminoids peaked at 1400 m a.s.l., climbers at 1700 m a.s.l., and woody species in the ranges of 2000-2500 m a.s.l. This provides insights on the difference of their relative response to environmental factors and at the same time a sort of consistency in their group response as opposed to the total number of species. Regarding mechanisms that structure richness at the landscape level water-energy dynamics, species area-relationships

due to physical shape of the mountain, local topographic and soil conditions play an important role. To fully realize the potential of deconstructive approach on the investigation of richness pattern, further deconstruction of growth forms and covering full range of the mountain summits is recommended. Woody species can further be dissected into trees and shrubs while graminoids are still heterogeneous and can be boiled down to a number of possible classes (e.g. grasses, sedges, annuals, perennials, etc.).

Plant functional types response along environmental gradients: The categorization of Plant functional types proves to be crucial to identify important environmental filters that structure diversity at the landscape scale. The results of **Manuscript 2** show that local topography (altitude and slope), soil texture and organic carbon play an important role in differentiating the relative abundance of PFTs in the landscape. These natural gradients of topography and soil properties combine the variation in climatic parameters (e.g. temperature, rainfall), disturbance effects, and resource availability. The classification we employ in our study system into four major categories (growth forms, stress/grazing, temporal attributes and water/nutrient) conceives a number of vegetation strategies to ecosystem responses. The growth forms are generally related to adaptation to climatic constraints and hence affect the structure and diversity of ecosystems. Thus, they provide information about the predominant role of climate as a factor in structuring the distribution and abundance of plant functional types. Concerning response to physical and biotic stressors along gradients, possession of armature and tussocks were selectively favoured in drought stressed lowland environments while rosettes and rhizomes were abundant in high altitudes where adaptation to chilling was a selective factor.

Plant functional types related to temporal attributes of vegetation such as leaf phenology (shedding of leaves) and life longevity (annual vs. perennial) address the effect of seasonal rhythm of climatic events and nutrient conservation (e.g. leaf nitrogen concentration), differential allocation of carbon on growth or reproduction. For instance, a relatively higher abundance of deciduous woody species in the lowlands in our study area demonstrates that vegetation show adaptations to seasonal changes in climate conditions. During the dry seasons woody species shed leaves to reduce moisture loss and absorb leaf nitrogen before the loss of foliage (Bonan 2008). Finally, mode of access to resources and water storage were found to be important vegetation strategies in our study system. Succulent species were more abundant in lowlands where water shortage should be an adaptive obligation. Diaz & Cabido

(1997) reported similar results in the semi-arid lowlands of south-west Argentina where succulence as a strategy to store water and buffer the effect of drought in lowland areas. Symbiotically nitrogen fixing plant functional types were abundant in lowlands where soil organic carbon was low (**Manuscript 2**).

Though we were interested to classify the whole vegetation into simple and sizeable PFTs, our approach was not able to capture some strategies which could probably be very important in our study area as well. This is particularly true for categories, stress/grazing and nutrient/water related traits, for the two groups we have simply assigned a "no adaptation" for those species which might use some other strategies to capture resources or responses to specific physical and biotic stressors. The rooting depth, degree of ramification and other drought avoidance or tolerance strategies could help to capture the whole system. Some studies (Skarpe 1996) indicated that rooting depth is important trait which affects the performance of plants in the semi-arid and arid environments. In addition, the role of disturbance in structuring the abundance of plant functional types should be incorporated to elucidate clear picture of PFTs response along environmental gradients. Nevertheless, our results can be used as a data base for future attempts of understanding PFTs response to environmental gradients in areas of similar settings.

Drivers of biodiversity loss: The results of **Manuscripts 3 and 4** reveal the major threats of biodiversity loss (land use and climate change) and potential ecological consequences on the vegetation of the study area. The effect of land use change is clearly evident in the Ethiopian highlands and the nearby Rift Valley where the natural vegetation has suffered habitat destruction due to increasing human population in the last few decades (**Manuscript 3**). In a recent study Vivero *et al*. (2006) reported that 137 (13% of the total estimated woody taxa of the country), 376 herbs, 57 succulents, 12 climbers and 8 epiphytes from the flora of Ethiopia and Eritrea have been included in the red list category of the IUCN.

The potential ecological consequences such as lowland biotic attrition, range shifts and contractions, and extinction are likely phenomena due to climate change in the study area (**Manuscript 4**). The potential shifts in species ranges (and hence PFTs) could possibly result in the restriction of ecological functions (e.g. nitrogen fixation). Climate change may also impact the disturbance regimes (e.g fire cycles in semi-arid ecosystems) and influence biotic interactions in the landscape. These processes would eventually drive species extinctions and

loss of their ecological functions and services, particularly endangered and endemic species will be severely affected. Thus, the projected rapid rise in temperature combined with habitat loss and fragmentation, will have a potential negative consequences on the biodiversity of the study area.

In conclusion, this study capitalizes on the application of plant functional types to the study of vegetation response to environmental factors in tropical high mountains. It is in fact the functional attribute of a species which interacts with the environment and determines the response of vegetation to external environmental conditions than the species *per se*. Hence, PFTs provide hints as to how and why certain species co-occurred in ecological communities and would help to explain patterns of species diversity. Moreover, deconstruction of species richness into relatively homogenous plant functional types (growth forms) deciphers the emergent pattern of diversity and mechanisms structuring them along altitudinal gradients. The identification of emergent patterns and attributing them to mechanistic explanations are pre-requisites for conservation planning to save biodiversity of the study area. The study also clearly showed that land use/land cover change and global warming will pose threats to biodiversity of the region. Conservation of biodiversity in the future warmed climate requires consideration of the effect of land use and climate change on species responses. Consequently, nature conservation strategies and future reserve designs should consider options for human assisted migration across fragmented landscapes and creating dispersal routes for species to track to new thermal niches.

The following two issues were identified for further research to fill future research gaps:

1. Disturbance is one of the ubiquitous elements in the landscapes and attempts of identifying biodiversity pattern should properly consider the extent and properties of disturbance as the driver of biodiversity. There is a clear deficit of information on the role of disturbance as driver of diversity pattern at landscape level, particularly in the semi-arid Rift Valley regions of Ethiopia.

2. The dispersal abilities of species and the roles of dispersal agents are critically needed to understand the pattern of diversity distributions in the face of land use change and global warming. The high share of species at risk of range shift gaps demands, therefore, detailed exploration of potential natural dispersal abilities of species.

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List of Manuscripts and Specification of Own Contribution

"Writing" refers to the actual formulation of sentences and paragraphs. Comments and inputs from discussions with the co-authors are covered under "discussions". Proof-reading and language editing was done by professionals for each manuscript.

Manuscript 1

Authors	Desalegn Wana & Carl Beierkuhnlein
Title	**Plant species and growth form richness along altitudinal gradients in the southwest Ethiopian Highlands**
Status	Submitted (ID-JVS-A-00354)
Journal	Journal of Vegetation Science (20. 06. 2009)

Contributions

Desalegn Wana	data collection (100%), data analysis (100%), writing (100%), discussions (90%), corresponding author
Carl Beierkuhnlein	discussions (10%)

Manuscript 2

Authors	Desalegn Wana & Carl Beierkuhnlein
Title	**The relative abundance of plant functional types along environmental gradients in the southwest Ethiopian highlands**
Status	resubmitted after incorporating major revisions (ID-JTE-09-248)
Journal	Journal of Tropical Ecology (11. 08. 2009)

Contributions

Desalegn Wana	data collection (100%), data analysis (100%), writing (100%), discussions (75%), corresponding author.
Carl Beierkuhnlein	discussions (25%)

Manuscript 3

Authors	Desalegn Wana, Giriraj Amarnath and Carl Beierkuhnlein
Title	**Land use/land cover change in the South-western Ethiopian highlands**
Status	in preparation
Journal	Journal of Mountain Research and Development

Contributions

Desalegn Wana	data collection (100%), data analysis (30%), writing (100%), discussions (80%), corresponding author.
Giriraj Amarnath	data analysis (70%), discussions (10%)
Carl Beierkuhnlein	discussions (10%)

Manuscript 4

Authors	Juergen Kreyling, Desalegn Wana & Carl Beierkuhnlein
Title	**Climate warming and tropical plant species – consequences of a Potential upslope shift of isotherms in southern Ethiopia**
Status	in preparation
Journal	Diversity & distributions

Contributions

Juergen Kreyling	data analyses (80%), writing (60 %), discussions (60%)
Desalegn Wana	data collection (100%), data analysis (20%), writing (40 %), discussions (30%)
Carl Beierkuhnlein	discussions (10%)

Journal of Vegetation Science, submitted (ID-JVS-A-00354)

Plant Species and Growth Form Richness along Altitudinal Gradients in the Southwest Ethiopian Highlands

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Abstract

Questions: Do growth forms and vascular plants richness follow similar patterns along the altitudinal gradient? What are the driving mechanisms that structure richness patterns at the landscape scale?

Location: South-western Ethiopian highlands

Methods: Floristic and environmental data were collected from seventy four plots with 400 m^2, which were distributed along altitudinal gradients. Boosted regression trees were used to derive the patterns of richness distributions along altitudinal gradients.

Results: Total vascular plant richness did not show any strong response to altitude. Contrasting patterns of richness was observed for several growth forms. Woody, graminoids and climber species richness showed a uni-modal structure. However, each of these groups had a peak of richness at different altitudes: graminoid species partitioning at a lower elevation, then climbers and finally woody species at a higher elevation. Fern species richness increased monotonically towards a higher altitude, but herbaceous richness had a dented structure at mid-altitude. Soil sand fraction, silt, slope and organic matter were found to

contribute a considerable amount of the predicted variance of richness for total vascular plants and growth forms.

Main Conclusions: Hump-shaped species richness patterns were observed for several growth forms. A mid-altitudinal richness peak was the result of the combination of climate related water energy-dynamics, species area-relationships and local environmental factors which have direct effects on plants physiological performance. However, altitude represents the composite gradients of several environmental variables that are interrelated. Thus, considering multiple gradients would help to reveal a better picture of richness and the potential mechanisms that structure the distributions of biodiversity in high mountain regions of the tropics.

Key words: Boosted regression trees, ß-diversity, Geodiversity, Tropical mountains

Introduction

Understanding how biodiversity is organized across space and time has long been a central concern of ecologists and biogeographers. There exists a gradient of diversity distributions across multiple spatial scales (Brown & Lomolino 1998; Field *et al.* 2009). Latitudinal gradients and the island pattern of diversity (the species-area relationship) are the most conspicuous patterns and hence attempts have been made to document and account for the underlying mechanisms of such observed gradients (Gaston 2000; Whittaker *et al.* 2001).

Altitudinal patterns of diversity are poorly understood (Sanchez-Gonzalez & Lopez-Mata 2005). As a consequence of expected climate changes, ecologists and biogeographers are motivated to investigate these patterns and analyse their underlying mechanisms (Grytnes 2003; Jentsch & Beierkuhnlein 2003; Sanchez-Gonzalez & Lopez-Mata 2005; Zhao *et al.* 2005). Generally, species richness tends to decrease with altitude (Bruun *et al.* 2006).

Nevertheless, several studies have also documented a non-monotonic pattern of species richness (Rahbek 1995; Bhattarai & Vetaas 2003). The most commonly observed pattern of diversity is a mid-altitudinal bulge (Rahbek 2005; Zhao *et al.* 2005). There is evidence of a mid-altitudinal trough in species richness gradients along altitude (Peet 1978) in the semiarid eastern slope of the Front Range, USA.

Altitude is a proxy variable for water-energy dynamics in mountain ecosystems (O'Brien 1998; O'Brien *et al.* 2000). In addition to this, mountain environments are characterized by heterogeneous site conditions or relief effects with their impacts on soil, microclimate, and aspect (Jentsch & Beierkuhnlein 2003). Altitudinal ranges also provide compressed ecological zones (Körner 2000), which serve as 'rescue effects' (Lomolino 2001) for species along the transition zones.

Marquet *et al*. (2004) argued that any attempt to explain mechanisms that structure the pattern along spatial gradients (e.g. altitude) needs to break down the different components of diversity. They pointed out that functional attributes of species (e.g. physiological, life history and ecological attributes) are directly related to the aspect of the physical environment. Thus a proper understanding of the mechanisms that generate and maintain diversity at different spatial scales requires diversity measures to be divided into different components.

A study by Bhattarai & Vetaas (2003) in the Himalayan range indicate that woody species display a uni-modal pattern of diversity. Fern diversity declines with altitude (as a function of Potential Evapotranspiration) while herbaceous species (herbs, forbs, grasses) do not show any relationship to altitude. Bruun *et al*. (2006) report a uni-modal pattern of diversity for vascular plant richness and yet a marked difference in pattern for different functional groups (dwarf shrubs, trees, forbs and herbs). However, Sanchez-Gonzalez & Lopez-Mata (2005), in

the Sierra Nevada, Mexico, report a uni-modal pattern of diversity distribution for both life-form categories (trees, shrubs and herbs) and total vascular plant species richness.

The literature cited above indicates that there is no such consistent form and structure in the pattern of richness distribution along altitudinal gradients. It is possible however that different mechanisms may support different components of diversity distributions (Stevens *et al.* 2003; de Bello *et al.* 2006). This study aims to answer the following questions: 1) what kind of responses in richness patterns (unimodal or monotonic) are observed along the altitudinal gradient? 2) Do various growth forms and total vascular plant richness follow similar patterns along the altitudinal gradient? And, finally 2) what are the driving mechanisms that structure patterns of richness along the altitudinal gradient in the investigation area?

Methods

Study area

The study area is located at 5^{o}42'N-6^{o}20'N and 37^{o} 17'E-37^{o} 59'E (Fig 1) in the southwest Ethiopian highlands. The landscape includes different physiographic features such as plateaus, escarpments, a block mountain, undulating plains, and a graben where Lake Abaya and Lake Chamo are located. The topography of the Rift Valley consists of hills, as well as flat and faulted structures (Mohr 1971; Zanettin *et al.* 1978). The eastern boarder is marked by the Amaro horst, a block mountain that emerged during the formation of the Rift Valley (Levitte *et al.* 1974).

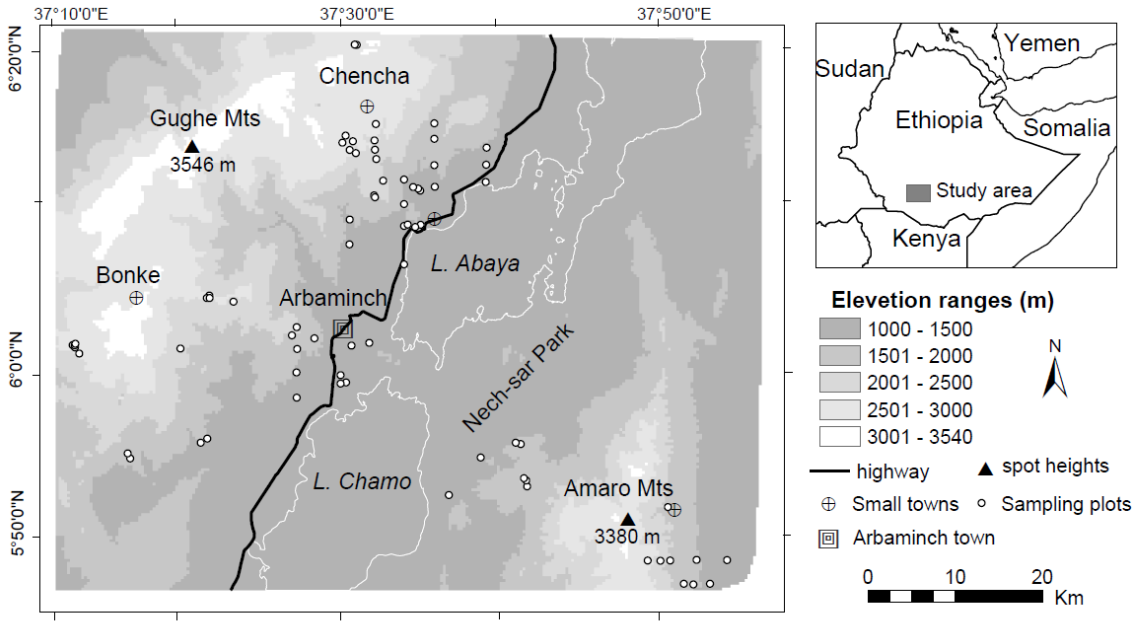

Figure 1: Location map of the study area

Rainfall in the study area shows a pronouncedly bimodal seasonal distribution (Fig. 2). The mean annual rainfall recorded over the last two decades, though not continuous, for the two stations, Arbaminch (1200 m) and Chencha (2700 m), was 888 mm and 1235 mm, respectively. The main rainy season, which accounts for about 40 % of the mean annual rainfall, occurs in April and May, while the lesser rainy season is in September and October. Arbaminch experiences a more pronounced dry season and receives less rainfall because of its low altitude and its rain-shadow position with regard to the moisture-bearing south-east trade winds that prevail in the spring and autumn seasons of the northern hemisphere. While a water deficit is prevalent in Arbaminch, that is except for in the months of April and May (Fig. 2a), the Chencha Highlands receive excess rainfall and a surplus is expected continuously for several months from April to October (Fig. 2b). The vegetation of the study area lies within the Somali-Masai regional centre of endemism (White 1983) comprising savannah grassland, bushland, dense thickets, riverine and groundwater forests, and in the Gughe and Amaro mountains broad-leaved afromontane rainforests (Friis 1992).

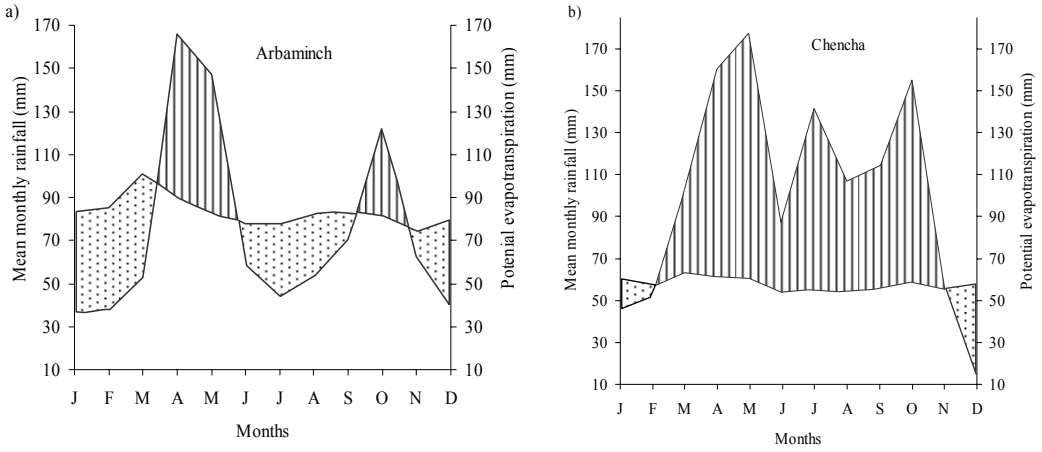

Figure 2: Climate diagram of Arbaminch (a) and Chencha (b) after Thornthwaite (vertical hatching indicate surplus while dot pattern indicate deficit). Arbaminch lies at 1200 m, mean annual temperature = 23°C, total Annual rainfall= 888 mm recorded. Chencha station is located at 2700 m, mean annual temperature = 14°C, total annual rainfall = 1235 mm, PET stands for potential evapo-transpiration. Arbaminch station had a temperature record from 1976 to 2005 and rainfall record from 1987 to 2005. Chencha had a temperature record from 1972 to 1981 while rainfall recorded from 1972 to 2004. However, rainfall records were not continuous and data were missing for Chencha from 1981-1989. All climate records were obtained from the Ethiopian National Meteorological Services Agency (NMSA).

Sampling scheme

The sampling design was based on the relative distribution of elevation along altitudinal gradients. SRTM digital elevation data sources were consulted to establish a digital elevation model (DEM) for the study area (Jarvis *et al.* 2008). The spatial classification of elevation at an interval of 200 m was extracted from the DEM. The number of plots was then selected depending on the relative distribution of elevation for representative sampling following a similar pattern of elevation distribution along the Gughe-Amaro Mountains. A roughly equivalent percentage of plots were allocated to the corresponding elevation ranges (Table 1). However, for the elevation band between 1000 and 1200 m a.s.l. where a lot of the area (~700 km ²) is covered by the two lakes, only 10. 8 % of the plots were sampled from 22. 8 % of the total area (Table 1). When the lakes area is excluded, which does not have any terrestrial vegetation, the total area in this range will be reduced by more than a half (9.8 %) and hence the percentage distribution of plots is roughly in a comparable range (Table 1). No sampling

was carried out above 3000 m a.s.l. due to problems with access and logistics. For each of the 200-meter ranges (10 altitudinal ranges between 1000 and 3000 m a.s.l.), sampling was conducted randomly depending on the presence of forest, woodland or any category of vegetation in the landscape. Agricultural fields and plantations were not sampled. In total 74 plots each with a size of 20 m x 20 m were set up following altitudinal gradients (see Fig. 1), from which plant species and environmental data were collected.

Table 1: The proportional distribution of area, plots and number of species observed along respective altitudinal ranges (475 species were encountered during sampling).

Ellevation ranges (m)	Area (km^2)	% Area	Number of plots	% Plots	Number of species	Average no. of species/plot
1000--1200	403.9*	9.8	8	10.8	125	16
1201--1400	1029.1	24.8	16	21.6	188	12
1401--1600	602	14.5	11	14.9	139	13
1601--1800	399.7	9.7	7	9.5	95	14
1801--2000	335	8.1	6	8.1	106	18
2001--2200	244.7	5.9	5	6.8	122	24
2201--2400	196.8	4.8	5	6.8	92	18
2401--2600	235.4	5.7	7	9.5	122	17
2601--2800	270.3	6.5	5	6.8	54	11
2801--3000	239.4	5.8	4	5.4	98	25
3001--3200	129.2	3.1	-	-	-	-
3201--3400	52.6	1.3	-	-	-	-
3401--3546	3.6	0.1	-	-	-	-
Total	4141.7	100.0	74	100	475	

* The total area in this range was 1103.9 km^2 including lake surface (700 km^2) we deducted the lakes area from the analysis as it does not contain any terrestrial vegetation.

Vegetation and environmental data

Fieldwork was carried out in two phases, from November 2006 to January 2007, and in December 2007, respectively. Both fieldwork phases were conducted after the small rainy season in the study area. Nevertheless, delays and early termination of the rains proved to be obstacles in the climatological timing. During the first fieldwork period, the rainy season

extended until mid-December while in the second period there was an early onset of the dry season in November 2007. However, such variations are to be expected and we do not expect this to have any significant impacts on the results of our study.

During the fieldwork 475 plant species were encountered. For those species that could not be identified precisely in the field, pressed specimens were taken back to the National Herbarium at Addis Ababa University for identification or confirmation. The nomenclature follows the published flora volumes of Ethiopia and Eritrea (Hedberg & Edwards 1989; Edwards *et al.* 1995; 1997; 2000; Hedberg & Edwards 1995; Hedberg *et al.* 2003; 2004).

Altitude and aspect were recorded using a Garmin GPS 3.1, and the slope was recorded using a clinometer. Aspects were coded prior to analysis following (Zerihun *et al.* 1989). In order to estimate stone cover, plots were divided into four and stone cover for each sub-quadrate was visually estimated and averaged to yield the percentage stone cover for a given plot. Five soil samples (0-30 cm depth) were collected from each corner and centre of the plot and mixed to produce a composite soil sample. These soil samples were analyzed for soil organic matter, texture, total nitrogen and available phosphorous in the analytical service laboratory of the International Livestock Research Institute (ILRI) in Addis Ababa, while the second batch of soil samples were analyzed in the Debre Zeit Plant and Soil Laboratory of the Ethiopian Agricultural Research Organization. Nitrogen was analyzed using the Kjeldhal method, phosphorous by applying the Bray method, texture by implementing the hydrometer method, and organic matter by following the Walkey and Black wet-oxidation method.

We have made a separate analysis of linear ordination techniques (RDA) using CANOCO 4.5 (ter Braak & Smilauer 2002) and checked for a multicolinearity effect of the environmental variables via their variance inflation factor and only clay had a variance inflation factor of 0.

The interest correlation result from ordination analysis has also shown that total nitrogen was highly correlated with organic matter (~0.7) (results not shown). Therefore, these two variables were excluded from the analysis. Information for bedrock was derived from a geological map of the Ethiopian Rift by Kazmin & Berhe (1981) at a scale of 1:500,000. Plots were then distributed over the map and bedrock information such as alkaline/sub-alkaline basalts, lacustrine, alluvium deposits, and gneisses was extracted.

Data Analysis

Data analyses were carried out using boosted regression trees, which have recently been considered to have a superior predictive performance compared to most traditional regression models (Elith *et al.* 2008). Boosted regression trees combine tree based models from classification and regression trees and boosting techniques. Classification and regression trees have been used to model complex ecological data, which are generally characterized by non-linear relationships, complex interactions and missing values (De'ath & Fabricius 2000). The decision tress partition the predictor space into rectangles using a serious of rules having homogeneous responses to predictors (Elith *et al.* 2008). This homogenously partitioned rectangular space will then be fitted by a mean response value by a regression tree for observations in that region (De'ath & Fabricius 2000; Elith *et al.* 2008). In addition, classification and regression tree approach do not require data transformations, handles the effect of missing values in both the response and explanatory variables (De'ath & Fabricius 2000).

Boosting is an optimization procedure by which the loss of predictive performance or deviance of the model is minimized through sequential stage wise fitting of the regression tree. The first tree is the one which captures the largest variance in the response and all other

successive trees fit on the residuals without affecting the previously fitted regression trees (Elith *et al.* 2008). Moreover, boosted regression trees are able to combine the following advantages for modelling the distribution of species richness and relative abundance: stochasticity (bag fraction), learning rate and tree complexity. Boosted regression employs a stochastic process by which a random subset of data to fit each successive regression trees and hence reduce the variance of the final model (Elith *et al.* 2008). For instance, if the bag fraction (probability) of 0.5 is set to run the model, it takes a random subset of 50 % of the predictors to model each successive regression trees.

The learning rate which is known as the shrinkage parameter controls the contribution of each tree in the model and generally the slower the learning rate the better the model fit will be. Nevertheless decision on the amount of the learning rate depends on the availability of computation time and the size of the data. The tree complexity (the number of nodes in a tree) controls the interaction terms of the variables in the model (Thuiller *et al.* 2006; Elith *et al.* 2008).

We have employed boosted regression tree analysis by using the free statistical software R version 2.7.1 (R Development Core Team 2008). We have used a default bag fraction of 0.5, a Poisson error distribution and a very slow learning rate (0.0005) and a tree complexity of 3 to model species richness distribution along environmental gradients. Elith *et al.* (2008) recommended a tree complexity of 2-3 and a slower learning rate for small data set. Species richness here is defined as the number of species encountered in a plot. Shared species were estimated based on EstimateS (Colwell 2005). Jaccard's beta diversity was computed using the formula: $ß = 1-[a\ (a + b + c)^{-1}]$ (Magurran 2004) while Weiher and Boylen (1994) beta diversity was computed using the equation: $ß = b + c$, where 'a' refers to the number of

species shared between two altitudinal ranges (sampling efforts) and 'b' and 'c' refer to species that only occur in the respective altitudinal ranges.

Results and Discussion

Altitudinal patterns of vascular plants and growth form richness

Our results showed that total vascular plant richness did not show any strong response to altitude effects in the regression model, despite its slightest increase with altitude (Fig. 3). However, the total number of species in each altitudinal range decreased with altitude (Table 1) and had a strong positive correlation with elevation zone area (Table 2). The average number of species per plot showed a weak positive correlation with altitude while it had a negative correlation with elevtion zone area (Table 2). Woody species richness tended to show a pattern with an increase that peaks at around 2000 m a.s.l. but then starts to decline and level off at higher altitudes above 2500 m (Fig. 3).

Table 2: The correlation coefficients of the relationships between altitude, elevation zone areas, average number of species and total number of species in a zone.

	Elevation zone areas	Average number of species in a plot	Total number of species in a zone
altitude	-0.72	0.53	-0.7
Elevation zone area	1	-0.63	0.89

Herbaceous species showed a dented structure at mid-altitude between 1500 and 2000 m a.s.l., i.e. they showed an increasing trend from 1100 to 1500 m, formed a depression at mid-altitude (1500-2000 m), and then continuously increased towards higher altitudes. By contrast, graminoid species richness showed a continuously declining pattern with altitude, albeit, showing maximum richness between 1100 and1400 m a.s.l. The climbers' richness

pattern was higher in the elevation ranges between 1100 and 1500 m and showed a decline at about 2100 m a.s.l. (Fig. 3). Unlike other growth forms described above, fern species richness increased consistently with altitude.

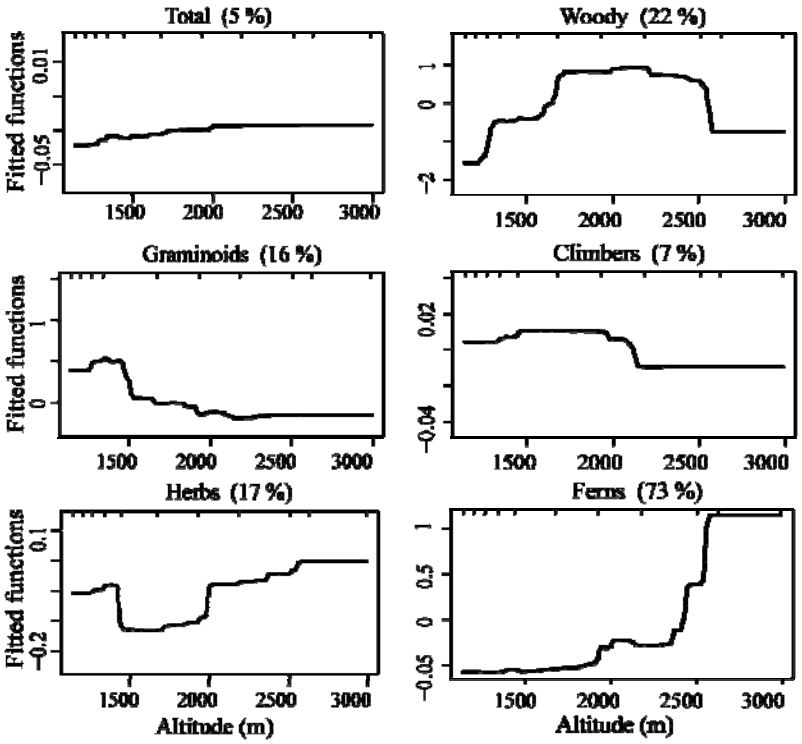

Fig. 3. Pattern of total species richness and growth forms along altitudinal gradients based on boosted regression tree with tree complexity 3, learning rate 0.0005, bag fraction 0.5 with Poisson error distribution, rug plots at inside top of plots show distribution of sites across specific variable in deciles (as in Elith *et al.* 2008). Percentage values in brackets indicate the relative amount of predictive variance explained by altitude from respective total variance for each group (see Table 3).

The combination of climate related water energy-dynamics, species area-relationships and local environmental factors which have direct effects on plants physiological performance (discussed in the next section) were important variables to explain the variations in richness distributions. Several theoretical (Huston 1994; O'Brien 1998; O'Brien *et al.* 2000; Rahbek 2005) and empirical researches (Bhattarai & Vetaas 2003; Grytnes 2003; Zhao *et al.* 2005) discussed the pattern of uni-modal structure of species richness along environmental gradients. The uni-modal structure of richness along altitude is primarily related to water-

energy dynamics or productivity (O'Brien 1998; Rahbek 2005)**.** Here, the interaction of temperature and water (e.g. evapotanspiration) affects the biological processes and competitive interaction among species and thereby affects species richness along the gradient (O'Brien *et al.* 2000).

The fact that ferns and herbaceous species did not display a humped structure in our study area could possibly be the effect of an incomplete gradient length. Some studies (Rahbek 1995; Bruun *et al.* 2006) pointed out that different patterns would be observed if an incomplete gradient length was studied compared to the whole gradient which covers the full length of species responses.

Lomolino (2001) argued that total number of species should be higher in the lower elevation zones because of species-area relationships. Along mountain slopes area tends to decrease with altitude. Hence, larger area in the lower elevation zones would be expected to support more heterogeneous environments, provide wider geographical ranges for species, and a lesser degree of isolation for potential immigrants (Lomolino 2001). By contrast the elevation zones in the higher altitude were smaller in area and characterized by a high degree of isolation and dispersal limitations. Romdal & Grytnes (2007) discussed the potential influence of surrounding elevation zone area as a regional pool of species on the local level richness. They found out a high correlation between the area within elevation band and species richness. The increase in the average number of species per plot, especially above 2000 m a.s.l., coincides with the high richness of woody species (Fig 3). Thus, it suggests that biotic interactions (e.g. competition and facilitation) could also play an important role in affecting the pattern of richness.

The relationship between richness and measured environmental factors

There were relatively higher cross validation correlation coefficients for ferns (0.71) and graminoids (0.53) followed by total vascular plant richness (0.46) and woody species richness (0.41) (Table 3). Herbaceous species and climbers had a lower cross validation correlation of 0.36 and 0.31, respectively. Among the variables considered in our study, altitude had the strongest influence on predicting the richness distribution of ferns (73 %), with a relatively low contribution to woody species (22 %), and herbs and graminoids (16 %) from the total explained variance in the measured environmental variables (Fig. 3). By contrast, altitude had a very weak predictive power in explaining richness patterns for climbers (7 %) and total richness (5 %).

Table 3. Summary statistics of boosted regression trees for total species richness and growth form categories. For all categories a tree complexity of 3 and learning rate 0.0005 were used, values in brackets are standard errors, CV = cross validation, sample size = 74.

Parameter estimators	Total	Woody	Herbs	Graminoids	Climbers	Ferns
Number of tress	2 800	3 250	3 150	4 550	2 350	7 800
Mean total deviance	108.62	22.44	3.74	4.329	1.976	1.243
Mean residual deviance	81.65	15.27	2.51	1.76	1.582	0.43
Estimated CV deviance	106.7 (20.3)	22.4 (4.1)	3.42 (0.6)	3.1 (0.4)	2.0 (0.4)	0.8 (0.2)
Training data correlation	0.596	0.662	0.67	0.801	0.59	0.827
CV correlation	0.46 (0.08)	0.41(0.12)	0.36 (0.1)	0.53 (0.1)	0.31(0.09)	0.71(0.05)

Soil texture (sand and silt fraction), organic matter and slope were found to be important parameters contributing to the predicted variance of richness for vascular plants and growth form categories in the study area. Species richness was found to peak at an intermediate level of soil sand fraction, organic matter and steep slopes (Fig. 4). In semi-arid environments, soil texture, especially sand, is important for better water holding capacity (Walter 1985; Breckle 2002) because of its buffering effect for evaporation as water infiltrates to sub-soil horizons. Soil organic matter also has multiple effects on soils such as the soil's physical structure, the

storage of nutrients, aeration and the stimulation of microbial activities (Tate III 1987) and may affect two important factors such as nutrients and soil moisture, which are important factors affecting the pattern of richness (Peet 1978; de Lafontaine & Houle 2007). At the higher altitude, because of low temperatures, organic matter would gradually decay and accumulate humus in the soils which may limit soil productivity and hence result in a low diversity of vascular plants (Sanchez-Gonzalez & Lopez-Mata 2005).

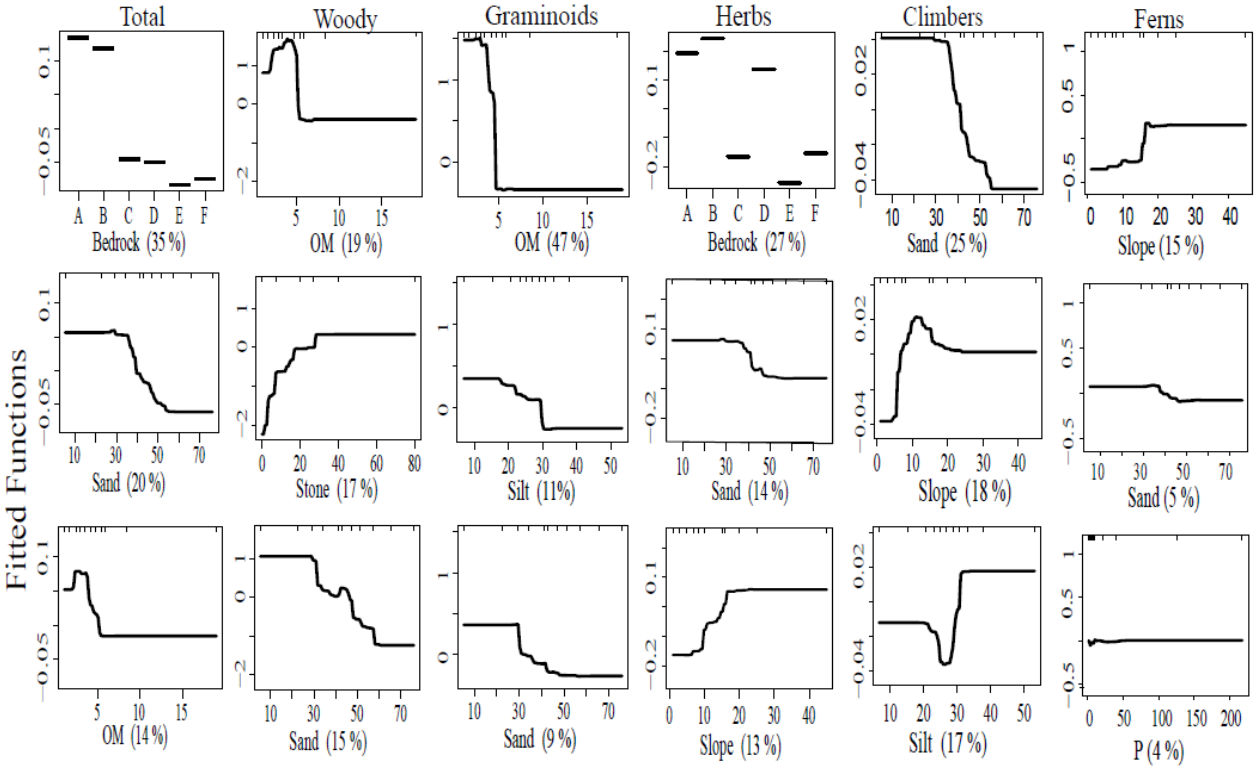

Fig. 4. The three environmental variables (excluding altitude which was separately shown in Fig. 3) predicting patterns of richness distribution for total richness and various growth form categories based on boosted regression tree with tree complexity 3, learning rate 0.0005, bag fraction 0.5 and Poisson error distribution, rug plots at inside top of plots show distribution of sites across specific variable in deciles (as in Elith *et al*., 2008, see text in the method sections for details). Percentage values in brackets indicate the relative amount of predictive variance explained by each variable from respective total variance for each group (see Table 3). (A= alkaline and sub-alkaline basalts, B = Gneisses and granites, C = alluvium deposits, D = Pleistocene basalt, E= Ryholites and trachytes, F = lacustrine deposits.

The difference in bedrock as a proxy indicator of the nutrient gradient accounts for more than a third of the total explained variance for vascular plants richness and about 27 % of the

variance for herb species richness (Fig. 4). High vascular plants richness was observed in alkaline to sub-alkaline basalts and gneisses while low richness was present in the alluvium and lacustrine deposits on the lower slope positions, especially along the Lakes Abaya and Chamo. A study in Swedish mountain areas indicated that bedrock heterogeneity (measured with Shannon's index) positively contributes in explaining the pattern of plant species richness and several plant functional groups (Bruun *et al.* 2003). As indicated in the description of the study area (Levitte *et al*. 1974; Zanettin *et al.* 1978; Kazmin & Berhe 1981), substrate heterogeneity is expected to play a significant role in explaining the variation of richness distributions across the landscape. The low richness of species observed in the lacustrine and alluvium deposits could possibly be due to nutrient-poor bedrocks compared to sodium/potassium (alkaline) and calcium-dominated alkaline bedrocks (Plagioclase) in the highlands where in-situ weathering releases essential nutrients for plant growth.

It appears that various patterns of richness distribution for vascular plants and growth forms can be accounted for by the interaction of multiple environmental gradients in the investigation area. Recently, studies conducted elsewhere (Le Brocque & Buckney 2003) reported the relationship of richness patterns with multiple environmental gradients. More recently, (Thuiller *et al.* 2006) applied the boosted regression tree analysis to model species richness within several biomes and regional scales in South Africa report the pre-eminence of topographic heterogeneity to structure richness pattern at the regional scale rather than water-energy dynamics.

Beta diversity along altitudinal gradients

There was high beta diversity along pairs of altitudinal ranges in the study area. It ranged from 0.57 to 0.98 (Table 4). The species composition turnover was more than 90 % among the four lower zones of altitudinal ranges (100-1600 m a.s.l.) and the upper four zones of altitudinal ranges of 2340-3000 m a.s.l. (Table 4). Weiher and Boylen's number of species between two pairs of altitudinal ranges as a measure of beta diversity showed that the total number of species between pairs of altitudinal ranges generally decreased towards higher elevation (Table 4, rows).

Table 4: Weiher and Boylen's number of species in two pairs of altitudinal ranges m a.s.l. (below the diagonal) and Jaccard's beta diversity for the same pairs (above the diagonal).

	Jaccard's beta (1-Jaccard's similarity)									
	1000	1200	1400	1600	1800	2000	2200	2400	2600	2800
1000		0.66	0.71	0.87	0.89	0.90	0.95	0.95	0.98	0.97
1200	153		0.57	0.78	0.79	0.84	0.90	0.94	0.97	0.96
1400	146	131		0.68	0.78	0.84	0.92	0.94	0.95	0.96
1600	168	179	120		0.68	0.76	0.82	0.93	0.94	0.93
1800	185	192	155	103		0.62	0.71	0.83	0.82	0.85
2000	203	222	187	133	102		0.66	0.79	0.86	0.84
2200	197	230	195	129	108	106		0.76	0.77	0.81
2400	225	276	231	187	162	158	130		0.76	0.75
2600	173	226	175	131	110	132	92	108		0.75
>2800	211	264	217	169	150	160	130	132	92	
	Weiher and Boylen's number of species									

The high beta diversity in the study area is contingent upon the combination of many altitudinal zonations of vegetation, high geo-diversity and human disturbances. The vertical zonation of vegetation is one of the most conspicuous phenomena in the east African Mountains (Friis 1992), mainly as a response from temperature and precipitation. This vertical zonation of vegetation would tend to support different plant communities and create an overall gradient of plant community turnover across the whole mountain ranges.

In regard to the geo-diversity, the structural, tectonic and geomorphic processes of the tertiary and quaternary periods resulted in the complex heterogeneity of the landscape. Consequently, various bedrocks with different ages and mineralogy were exposed to the surface within short distances, providing substrates for plants and hence encouraging a high turnover of species across the landscape. In a study conducted on the north-eastern edge of the main Ethiopian Rift Valley lithological discontinuity was responsible for plant community transitions along altitudinal gradient (Beals 1969).

Landscape fragmentation due to land cover conversion and related human disturbances appear to play an important role for the high beta diversity across the landscape. This was particularly true for the higher altitudinal zones above 2200 m a.s.l. where there were high human population densities and consequent fragmentation of forests for agricultural purposes. The decline of Weiher and Boylen's number of species with increasing altitude could partly be due to the effect of decreasing area with altitude and isolation of high mountains from the surrounding landmass and hence a higher dispersal limitation resulting in low rescue effects (Lomolino 2001). In addition, higher elevation zones (above 2200 m) were characterized by a high intensity of human disturbances (Desalegn & Zerihun 2005).

In conclusion, the pattern of richness observed in our study varied with several categories of growth forms. Generally, however, hump-shaped richness patterns were observed for several categories. Several factors such as climate related water energy-dynamics, species area-relationships, and local environmental factors may work in concert to produce such observed patterns. In addition, altitude represents composite gradients of several environmental variables which at times are inter-correlated (Rahbek 2005). A number of other environmental variables play a dominant role to explain the pattern of diversity at the landscape scale. At the landscape scale topographic (particularly slope) and substrate heterogeneity, as well as soil

properties capture the patterns of species richness along elevation gradients. Disturbance regimes, which were not considered here, may also play a considerable role in structuring the pattern of diversity distributions in anthropogenically modified landscapes. Thus, considering multiple gradients would help to reveal better pictures of richness patterns and the potential mechanisms that structure the distributions of biodiversity in high mountain regions of the tropics.

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The relative abundance of plant functional types along environmental gradients in the south-west Ethiopian highlands

Running title: Plant functional types along environmental gradients

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ABSTRACT

Plant functional types across environmental gradients can be taken as a powerful proxy to reveal vegetation-environment relationships and response to global change. The objectives of this study were to evaluate the distribution of plant functional types along altitudinal gradient and to examine the relationship of plant functional types to environmental variables. The study was conducted in the Gughe-Amaro Mountains, in the south-west Ethiopian highlands. We established seventy four plots each with an area of 400 m^2 (20 m x 20 m). Data on site environmental conditions and abundance of plant functional types were analyzed using constrained linear ordination technique (RDA) in order to identify the relationships between plant functional types and environmental variables.

Altitude, soil organic carbon, soil sand fraction and surface stone cover were significantly related to the abundance of plant functional types across the gradient. Tussocks and thorns/spines were abundant in lower altitudinal ranges in response to drought while rhizomes and rosettes were abundant in the higher altitude in response to chilling. Topographic attributes (altitude and slope) and soil organic carbon play an important role in differentiating the relative abundance of plant functional types along the gradient. Thus, considering specific plant functional types would provide a clear understanding of the patterns of vegetation and their response to environmental gradients in the drought sensitive tropical regions of Africa.

Keywords: Africa, biodiversity gradient, functional traits, montane ecosystems, Rift Valley

INTRODUCTION

Across environmental gradients plant functional types (hereafter referred to as PFTs) can be taken as a powerful proxy to reveal vegetation-environment relationships. Plant functional types are defined as sets of species that demonstrate either a similar response to the environment or have similar effects on major ecosystem processes (Gitay & Noble 1997). This study focuses on the response of PFTs to environmental gradients. PFTs are grouped according to their morphological, physiological, regenerative or phenological features (Lavorel & Garnier 2002), rather than to their phylogenetic relationships. The common response of PFTs provides the opportunity to directly link functional response traits with environmental variables such as climate, disturbance regimes and resource availability (Hooper *et al.* 2002). This is why PFTs are a valuable tool for the monitoring of ongoing environmental changes.

Species develop a number of specialized traits as a possible mechanism of adaptation to environmental factors (e.g. aridity), disturbance and biotic interactions (Beierkuhnlein & Jentsch 2005, Cody 1991). The growth form provides essential information on the vegetation strategy regarding e.g. energy interception and water cycle (Baldocchi *et al.* 2004), carbon storage (Diaz & Cabido 1997) and support of static body weight against wind (Rowe & Speck 2005).

In semi-arid environments, such as in our study area, where water shortage is a limiting factor, plants are expected to develop morphological features such as thorns/spines to reduce heat loading in the leaves via reflection and absorption of solar radiation (Gates 1980), and water storage organs to buffer the effects of drought stress (Diaz & Cabido 1997). More importantly, the morphological features, such as thorns and spines (Roininen *et al.* 2007), serve as the defence organs to deter the effect of herbivory. Thus, these morphological features would help to reduce heat (Cornelissen *et al.* 2003) or drought stress in the semi-arid areas where moisture and thermal stresses are expected to be higher. Similarly, the life span (annual vs. perennial) of herbs and graminoids can be seen to reflect the timing of resource availability, resulting in a relatively large investment of annuals into reproductive traits compared to vegetative ones (Diaz & Cabido 1997, Silvertown 2004). Thus, plant functional types aggregate a variety of species responses to the environment and are powerful input data for global land-cover modelling (Leemans 1997).

Though the use of PFTs has been well recognized in ecosystem response and global change modelling, few studies have so far investigated the relationship of PFTs to environmental gradients in the African tropics (Skarpe 1996). Most available studies are located in temperate climates (de Bello *et al.* 2006, Diaz *et al.* 1999, Stevens *et al.* 2003) and the neotropics (Condit *et al.* 1996; Kraft *et al.* 2008). This study aims to evaluate the distribution of PFTs along altitudinal gradient and to examine the linkages between PFTs and measured environmental variables. Specifically the paper intends to address the following hypotheses: 1) Altitude and slope have a significant effect on the variation of the relative abundance of plant functional types in the study area; 2) soil texture and fertility have a strong explanatory power to the variation in the relative abundance of plant functional types along altitudinal gradients; 3) PFTs response to stress (drought and chilling) and grazing would favour the abundance of distinct plant functional types such as thorny and tussocks in the lowlands vs. rosettes and rhizomes at higher altitudes.

METHODS

Study area

The study area is located at 5° 42'--6° 20' N and 37° 17'--37° 59' E (Figure 1), about 500 km south of the Ethiopian capital, Addis Ababa. The physiography of the investigation area is characterized by a great diversity that is related to the genesis of the Rift Valley. This landscape includes plateaux, escarpments and undulating plains where Lake Abaya and Lake Chamo are located.

The eastern border is marked by the Amaro horst, a block mountain that emerged during the formation of the Rift Valley. The western escarpment of the Rift Valley down from the Chencha Highlands is characterized by steep slopes and a topography that is greatly dissected by small streams, which flow into Lake Abaya and Lake Chamo. The highlands of Gughe consist of Tertiary volcanites (Zanettin *et al.* 1978), while the Rift Valley is largely filled with Quaternary deposits (Mohr 1971). The Amaro Mountains on the eastern border of the study area are dominated by uplifted crystalline rocks, composed of gneisses and granites (Levitte *et al.* 1974).

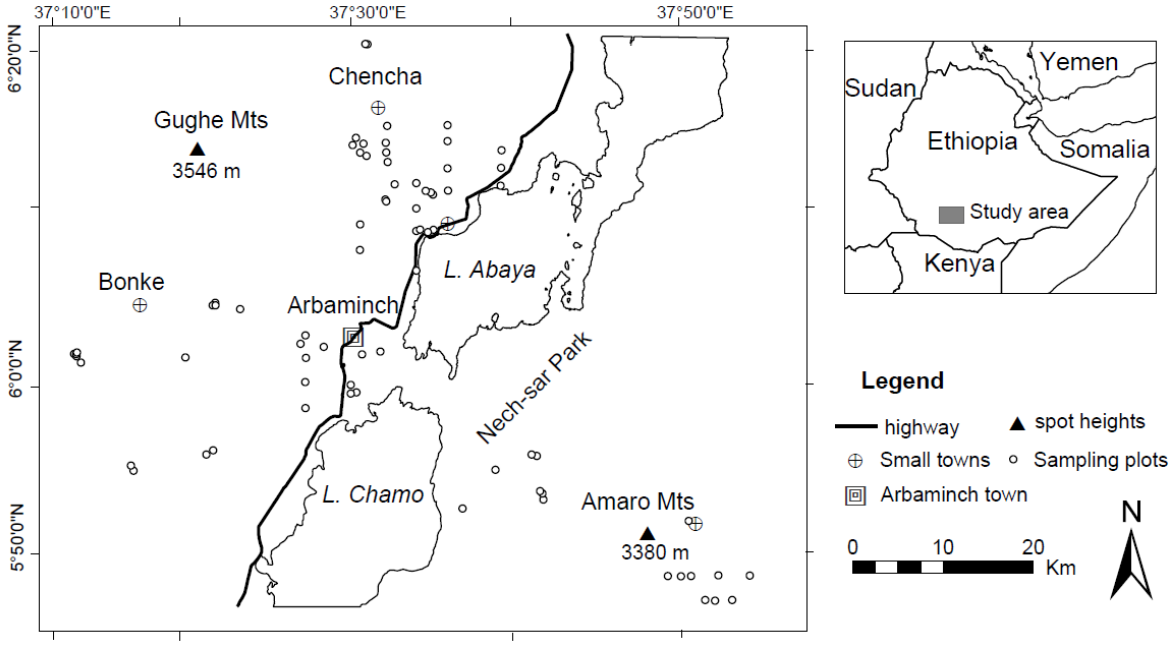

Figure 1: Location map of the study area

Rainfall in the study area shows a pronouncedly bimodal seasonal distribution. The mean annual rainfall recorded for Arbaminch (1200 m) in the period from 1987 to 2005 was 888 mm while for Chencha (2700 m), for the period 1972 to 1980 and 1990 to 2004, 1235 mm were recorded (Figure 2). The main rainy season, which accounts for about 40% of the mean annual rainfall, occurs from April to June, while the lesser rainy season is in September and October. Arbaminch experiences a more pronounced dry season and receives less rainfall because of its low altitude and its rain-shadow position with regard to the moisture-bearing south-east trade winds that prevail in April/May and September/October months in the region. During the aforementioned months Arbaminch experiences water surplus (Figure 2a), while the Chencha Highlands receive excess rainfall and a surplus is expected for the months from April to October (Figure 2b). Thus, this area combines the long-term climatic constancy of the tropics with seasonal variability and the permanent occurrence of tectonic and volcanic activity and disturbance.

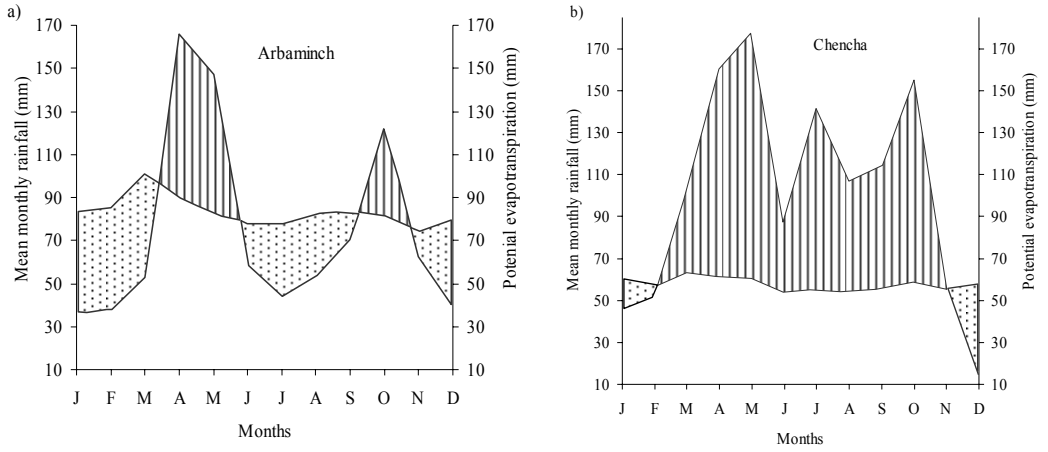

Figure 2: Climate diagram of Arbaminch (a) and Chencha (b) after Thornthwaite (vertical hatching indicate surplus while dot pattern indicate deficit). Arbaminch lies at 1200 m, mean annual temperature = 23°C, total Annual rainfall= 888 mm recorded. Chencha station is located at 2700 m, mean annual temperature = 14°C, total annual rainfall = 1235 mm, PET stands for potential evapo-transpiration. Arbaminch station had a temperature record from 1976 to 2005 and rainfall record from 1987 to 2005. Chencha had a temperature record from 1972 to 1981 while rainfall recorded from 1972 to 2004. However, rainfall records were not continuous and data were missing for Chencha from 1981-1989. All climate records were obtained from the Ethiopian National Meteorological Services Agency (NMSA).

The vegetation of the study area is part of the Somali-Masai regional centre of endemism (White 1983). It comprises savanna grassland, bushland, dense thickets, riverine and groundwater forests, and in the Gughe and Amaro mountains broad-leaved afromontane rain forests (Friis 1992). The broad-leaved afromontane vegetation in the study area is highly fragmented due to human settlement. The remaining relatively dense vegetation cover is found in the escarpment of the Rift Valley and in the Netch Sar National Park. However, the recent wave of immigration to the Rift Valley due to high population pressure in the highlands and apparent poverty has resulted in the transformation and degradation of woodland vegetation in the Rift Valley (Desalegn 2007, Desalegn & Zerihun 2005)

Sampling scheme

The sampling design was based on the relative distribution of elevation along altitudinal gradients. Digital elevation model for the study area was constructed from Shattle Radar Topography Mission (Jarvis *et al.* 2008) data. The topographic data were void filled for missing information and made available for public use on the web page of International Centre for Tropical Agriculture (http://srtm.csi.cgiar.org). The spatial classification of

elevation at the interval of 200 m was extracted from the DEM. The number of plots was then selected depending on the relative distribution of elevation for representative sampling following a similar pattern of elevation distribution along the Gughe-Amaro Mountains (Table 1). A roughly proportionate percentage of plots were allocated to the corresponding elevation ranges with the exception of the elevation band between 1000 and 1200 m asl, where a large surface is covered by the two lakes. No sampling was conducted above 3000 m due to logistic problems and difficulties of access during fieldwork. For each of the 200-m ranges (10 altitudinal ranges between 1000 and 3000 m asl), sampling was conducted depending on the presence of forest, woodland or any category of semi-natural vegetation in the landscape. Agricultural fields and plantations were not sampled.

Vegetation and environmental data

Fieldwork was carried out in two phases, November 2006 - January 2007, and in December 2007, respectively. Both phases of fieldwork were conducted after the small rainy season. Nevertheless, delays and an early termination of the rains proved to be obstacles in the seasonal timing. During the first fieldwork period, the rainy season extended until mid-December while in the second period there was an early onset of the dry season in November 2007.

In total 74 plots, each with a size of 20 × 20 m, were established (Figure 1), where environmental data, plant species and presence-absence information was recorded. During field survey 475 plant species were encountered (Appendix). For those species that could not be identified precisely in the field, specimens were taken to the National Herbarium at the Addis Ababa University for identification or confirmation. Functional traits were recorded for every species, whenever possible, in the field for the following traits: thorns/spines, rosettes, N-fixing legumes, and succulence. Additionally, plant functional types regarding for example life span for herbs and graminoids (annuals vs. perennials), leaf phenology (deciduous vs. evergreen) for woody species, the presence of rhizomes/stolons and potential N-fixing legumes were checked with the published flora volumes of Ethiopia and Eritrea (Edwards *et al.* 1995, 1997, 2000; Hedberg & Edwards 1989, 1995; Hedberg *et al.* 2003, 2004).

Table 1. The proportional distribution of area, plots and number of species observed along respective altitudinal ranges in the Gughe-Amaro mountains (475 species were encountered during sampling).

Ellevation (m)	Area (km^2)	% area	No. of plots	% plots	No. of species
1000--1200	403.9*	22.8	8	10.8	125
1201--1400	1029	21.3	16	21.6	188
1401--1600	602	12.4	11	14.9	139
1601--1800	399.7	8.3	7	9.5	95
1801--2000	335	6.9	6	8.1	106
2001--2200	244.7	5.1	5	6.8	122
2201--2400	196.8	4.1	5	6.8	92
2401--2600	235.4	4.9	7	9.5	122
2601--2800	270.3	5.6	5	6.8	54
2801--3000	239.4	4.9	4	5.4	98
3001--3200	129.2	2.7	-	-	-
3201--3400	52.6	1.1	-	-	-
3401--3546	3.6	0.1	-	-	-
Total	4841.7	100	74	100	475

* total area including parts of the two lakes is 1103.9

Altitude and aspect were recorded using a Garmin GPS 3.1, and the slope was recorded using a clinometer. Aspects were coded prior to analysis following Zerihun *et al.* (1989). For stone cover, plots were divided into four subquadrats. Then it was visually estimated and averaged to yield the percentage of stone cover in a plot. Five soil samples were collected at 0-30 cm depth from each corner and from the centre of the plot and mixed to produce a composite soil sample.

Classification of plant functional types

Plant functional types were classified according to four categories. (1) The first category is based on the whole plant traits which is mainly adaptation to climatic constraints and competition (Cody 1991), resistance to strong winds and support of static weight such as self supporting or climbing (Rowe & Speck 2005). We differentiate the growth forms woody plants, herbs, graminoids, climbers and ferns. Epiphytes were excluded from analysis because they were few in number. Additionally, some of the ferns have also epiphytic habits. Ferns are a phylogenetic category. Yet, we considered them as distinct type because of their specific response to regulate water and differential response to water availability compared to other groups along altitude gradients (Bhattarai & Vetaas 2003). (2) The second category is based mainly on the particular response to physical and biotic stresses. The physical stress which we expect in our system would include chilling (low temperature in high-altitude areas) and drought in the semi-arid zones along the lower elevation zones while the biotic stresses

include herbivory, grazing and "reproductive success". (3) The third category is related to the fluxes of resources and how species respond to temporal changes in environmental conditions (e.g. seasonality). In this category woody species were subdivided into deciduous vs. evergreens while herbs and graminoids were subdivided into annuals vs. perennials. (4) Finally, traits which were related to access and storage of resources such as water and nutrients were applied and species were attributed to the groups of hemi-parasites, succulents and nitrogen fixers (Table 2).

Table 2. Plant functional types (PFTs) categories and number of species in each group.

Growth forms		Stress/grazing		Temporal attributes		Water and nutrients	
PFTs	No. of species	PFTs	No. of species	PFTs	No. of species	PFT	No. of species
Woody	176	Rosettes	11	Deciduous	37	Nitrogen fixers	56
Graminoids	42	Rhizomes/stolons	59	Evergreen	153	Succulents	37
Climbers	48	Tussocks	12	Annual	74	Parasites	7
Herbs	191	Thorns/spines	56	Perennial	211	'No adaptation'	375
Ferns	18	'No adaptation'	340				
Total	475		478[1]		475		475

1 Three species were double counted (one for thorns/spines and two species for rosette and rhizomes) thus the total number of species for this category yields 478 (The total number of species encountered in the field were 475).

Data analysis

Before data analysis the presence-absence data of species for each PFT were pooled to generate the total number of species for the corresponding PFT within each plot and then the proportion (%) of each PFT was calculated out of the total number of species in a plot. Thus, abundance is defined here as the proportion (percentage) of a given plant functional type from the total number of species belonging to all PFTs in a plot.

Soil data analysis

The soil samples were analyzed for soil organic matter and then converted to soil organic carbon by dividing the percentage soil organic matter by 1.72 (SOC) (Schumacher 2002). Texture, total nitrogen (TN), and available phosphorus (AP) were analysed in the analytical service laboratory of the International Livestock Research Institute (ILRI) in Addis Ababa, and the second batch of soil samples were analyzed in the Debre Zeit Plant and Soil Laboratory of the Ethiopian Agricultural Research Organization. Nitrogen was analyzed using the Kjeldahl method, Phosphorus by the Bray method, texture using the hydrometer method, and organic matter by following the Walkey and Black wet-oxidation method.

Statistical analysis

The PFTs and most environmental data were transformed into logarithmic (log(x+1)) scale for normality. However, soil sand and silt fraction had a normal distribution and thus were not transformed. A constrained linear ordination technique (RDA) was used to investigate the relationship of PFTs with environmental factors using the software CANOCO 4.5 (ter Braak & Smilauer 2002). Forward automatic selection and partial Monte Carlo permutation was used to test the significance of the relation between PFTs and environmental variables.

RESULTS

PFT-environment linkages

The measured environmental variables explained relatively large proportions of variance for temporal attributes (44.7%) and growth forms (37.4%) from the total inertia in the PFT data (Table 3). However, the total variance explained for PFTs related to stress/grazing and water/nutrient was relatively small (Table 3). The amounts of explained variance shared by the first two axes for stress/grazing and water/nutrients were 24% and 26%, respectively (Table 3).

The first axes for all categories of PFT data were strongly correlated with altitude and soil organic carbon. These two environmental variables were intercorrelated ($r = 0.58$, results not shown). On the other hand, soil sand fraction was strongly correlated with the second axes for

all categories of PFTs excepting growth forms. Slope inclination was strongly correlated with the second axis for the growth form based classification.

Table 3. Constrained linear ordination analysis (RDA) of plant functional types and amount of variance explained (species data were log (x+1)-transformed, scaling with inter-species correlations and standardized by species centring), PFTs refers to plant functional types.

Plant functional types	Axes	Eigen values	Cummulative % variance		Variance explained
			PFTs data	PFTs_environment relation	
Growth forms	1	0.269	26.9	71.8	
	2	0.085	35.3	94.4	0.374
	3	0.014	36.7	98.1	
	4	0.007	37.4	99.9	
Stress/grazing	1	0.19	19	71.2	
	2	0.049	24	89.6	0.267
	3	0.025	26.4	98.9	
	4	0.002	26.7	99.8	
Water/nutrients	1	0.215	21.5	76	
	2	0.047	26.3	92.7	0.283
	3	0.02	28.3	100	
	4	0	28.3	100	
Temporal attributes	1	0.275	27.5	61.5	
	2	0.159	43.3	97	0.447
	3	0.013	44.6	99.8	
	4	0.001	44.7	100	

Forward selection of environmental variables showed that altitude was found to have a significant effect (P = *0.002*) on the relative abundance of plant functional types for all categories (Table 4). Slope inclination was significantly related to growth form (P = *0.016*) and temporal attributes (P = *0.01*). Similarly, SOC was found to be significantly related to the relative abundance of growth forms (P = *0.002*) and temporal attributes (P = *0.01*) (Table 4). However, soil sand fraction had a significant effect only on the temporal attributes (P = *0.0006*) while surface stone cover was significantly (P = *0.012*) related to the relative abundance of PFTs attributed to stress/grazing (Table 4).

Table 4. The relationships among environmental variables and plant functional types based on Partial Monte Carlo permutation tests (** = significant at P ≤ 0.01, * = significant at P < 0.05); SOC stands for soil organic carbon, Alt = altitude, Stone = surface stone cover, C:N = carbon:nitrogen ratio, AP = available phosphorus).

	Growth forms		Stress/grazing		Temporal attributes		Water/nutrients	
Variable	F	P	F	P	F	P	F	P
Alt	20.5	0.002**	10.61	0.002**	23.1	0.002**	12.1	0.002**
SOC	7.05	0.002**	2.31	0.086	6.39	0.01**	1.92	0.136
slope	3.46	0.016*	0.84	0.508	3.21	0.034*	0.71	0.472
C:N	1.83	0.132	1.40	0.254	2.88	0.052	2.10	0.088
Silt	1.04	0.376	1.47	0.202	1.03	0.338	0.92	0.408
Sand	0.71	0.582	1.48	0.196	4.81	0.006*	2.16	0.128
Aspect	0.74	0.526	0.72	0.564	0.28	0.836	1.88	0.132
AP	0.47	0.724	0.55	0.696	1.21	0.314	0.29	0.808
Stone	0.30	0.876	3.32	0.012*	2.45	0.074	2.28	0.118

Graminoids (grasses and sedges) were highly negatively correlated with SOC but were positively related to available phosphorus (Figure 3a). Herbs were strongly related to slope inclination (Figure 3a) than altitude in the study area. Tussock grasses and thorny/spines in the study area were highly related to surface stone cover and available phosphorus and negatively related to altitude (Figure 3b). Rhizomatous and rosettes PFTs were found to be more abundant in areas of relatively higher altitude, higher soil sand content and low amount of soil available phosphorus (Figure 3b). However, for the group 'no adaptation', which we could not place our PFTs related to stress/grazing, appears to be positively correlated with soil silt fraction, SOC and aspect.

In regard to the abundance of PFTs related to temporal attributes (leaf seasonality and life span), the abundance of woody species was clearly differentiated between higher and lower altitudes (Figure 3c). Deciduous woody species were more abundant in lower altitude while evergreen woody species were abundant in the higher elevation zones (Figure 3c). Deciduous woody species showed a strong negative relationship to soil organic carbon and were positively related to surface stone cover, whereas evergreen woody species were positively related to soil sand fraction and SOC (Figure 3c).

Annuals and perennials (graminoids and herbs) were strongly correlated to aspect, slope inclination, and soil silt fraction. However, the pattern of abundance of annuals and perennials

was not clearly differentiated probably due to the aggregation of comparatively large groups such as graminoids and herbs.

In regard to PFTs related to nutrients and water acquisitions: nitrogen fixers were strongly correlated with higher surface stone cover and C:N-ratio whereas succulents showed a strong positive relationship to available phosphorus in the soil (Figure 3d). Hemi-parasites, however, did not appear to have any relationship to the measured environmental variables.

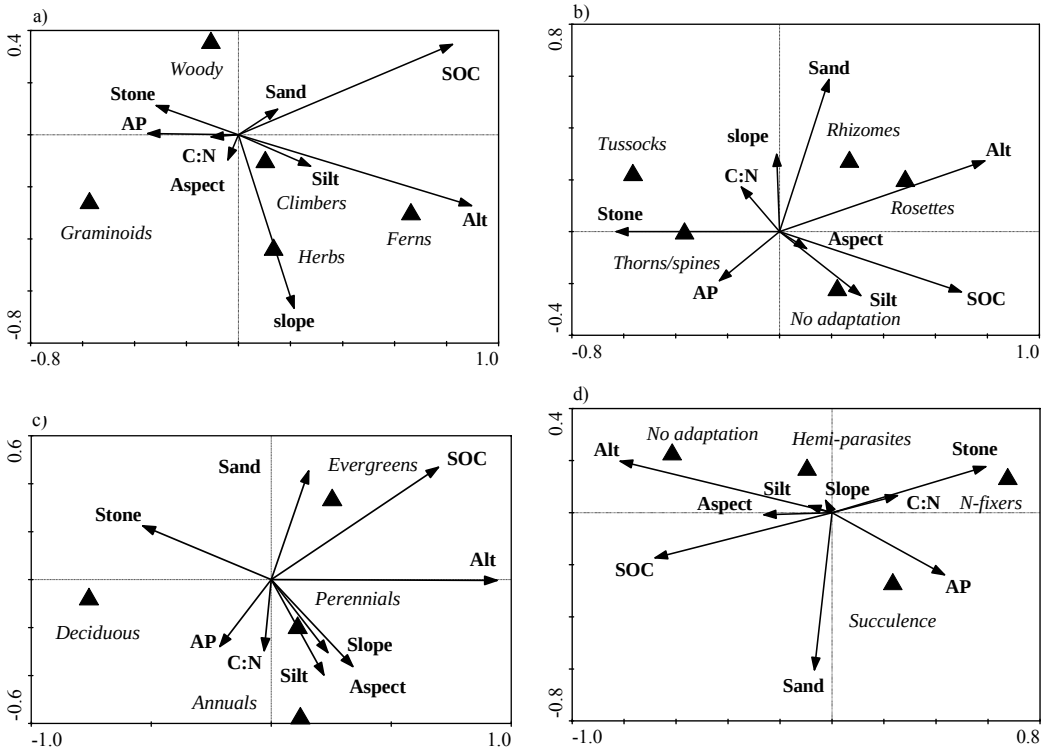

Figure 3: A redundancy analysis of plant functional types and environmental variables; growth forms (a), grazing/stress (b), temporal attributes (c) and nutrient- and water-related plant functional types (d); SOC = soil organic carbon, AP = available phosphorus, Alt = Altitude, Stone = surface stone cover.

DISCUSSION

Topographic relief (such as altitude, slope inclination and aspect exposition) and SOC played an important role in differentiating the relative abundance of PFTs across the landscape. The impact of topographic relief is apparent in water-energy distributions across spatial gradients, which in turn control photosynthetic processes (productivity) and thereby the diversity of woody species (O'Brien 1998, O'Brien *et al.* 2000). Altitude can be considered to be a proxy variable to the variation in the distribution of water and energy in high-mountain regions. In

addition, the range of altitude provides habitats for species across the gradient. The topographic heterogeneity of slopes and exposure (aspect) also affect the (re)distribution of vital resources such as water and solar energy. This is supported by the strong explanatory effect of slope inclination for growth forms and temporal attributes.

In mountain regions and in semi-arid ecosystems slope inclination and slope exposure (aspect) commonly play an important role in structuring the relative abundance of PFTs since the redistribution of water and nutrients is affected by the relative slope position (Breckle 2002, Walter 1985). Slope inclination and slope aspect are the most important factors affecting patterns of vegetation in the landscape. However, their role in the semi-arid environment is very critical in forming patchy vegetation and barren lands which in turn affects the run-on/run-off processes, soil depth, water retention and nutrient status of the soil (Pueyo & Alados 2007, Wilkinson & Humphreys 2006). It is reported that slope aspect has a strong relationship to productivity and to plant species composition (Gong *et al.* 2008). A study conducted by Teshome *et al.* (2004) in the Gamo Gofa region south of the current study area, reported low herbaceous cover in the steep-slope area dominated by a *Commiphora cyclophylla* plant community. Our study, however, showed a strongly positive correlation of herb abundance with slope inclination. This could probably be due to the high intensity of grazing in the gentle slopes which was not included in this study.

Plant species adopt different strategies to access water and nutrients in the environment. They modify rooting depth and resource segregation by timing and other mechanisms (Silvertown 2004). In our study graminoids (grasses and sedges) show strong negative correlations with SOC. This is apparent because the largest source for SOC is litter-fall from forest trees, while SOM (and hence SOC) replenishment in grass-dominated ecosystems mainly depends on the die-back of grass roots as a source of organic matter (Troeh & Thompson 2005). Graminoids showed a strong positive correlation to AP in the soil (Figure 3a) at the lower elevation range, probably due to low leaching in the semi-arid environments of the Rift Valley.

PFTs related to grazing/stress are clearly separated along altitudinal gradients. Tussock grasses and species with thorns/spines were abundant in the lower elevation zones where drought is expected to be a limiting factor while rhizomes and rosettes were found to be abundant in the higher elevation zones. The combination of drought stress with

grazing/herbivory over time tends to favour tussocks and thorns/spines while that of chilling and grazing/herbivory appear to favour rhizomes and rosettes (Figure 3d; Figure 4).

Various forms of tussock developments were favoured as adaptation strategies to environmental stress (Nishikawa 1990) and disturbance such as fire and grazing. Tussock formations in the semi-arid environments enhance survival by forming organic debris, fine soils and retain soil moisture (Pugnaire & Haase 1996). In addition, they buffer soil erosion along slopes. Thorns/spines help to reduce heat or drought stress (Cornelissen *et al.* 2003) by dissipating heat loading on the surface of the leaves and steams or absorbing solar radiation, in addition to their role as a mechanical deterrence against vertebrate herbivory (Grime 2001).

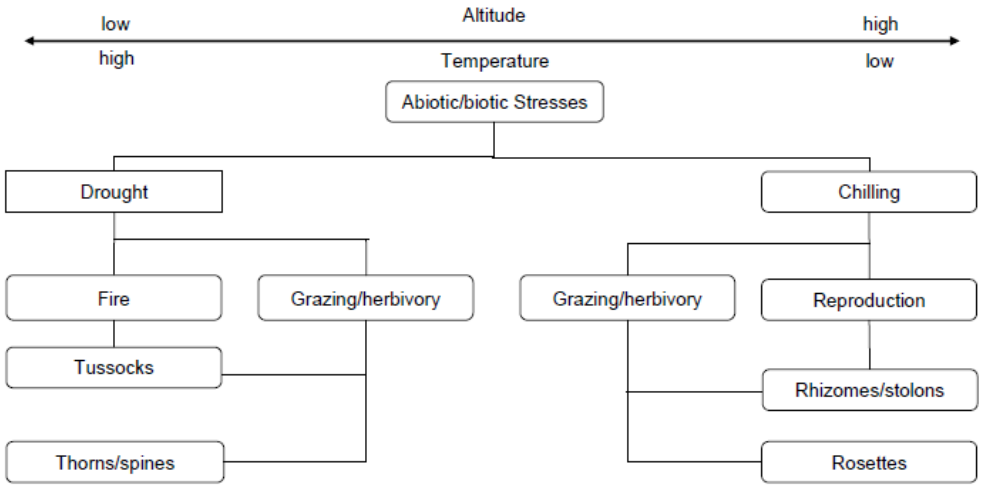

Figure 4: The response of PFTs to drought/chilling and grazing along altitudinal gradient.

Rhizomes and stoloniferous traits are features that are presumed to be related to reproductive success. They may help organisms to buffer the effect of unexpected occurrence of drought or frost (Diaz & Cabido 1997). If not being destroyed, rhizomes deliver the competitive advantage to re-occupy space after disturbance events (e.g. grazing or mowing) because of their ability to store metabolic products and hence quick re-sprouting (Diaz & Cabido 1997, Klimesova *et al.* 2008).

The abundance of deciduous woody species in the lower altitudes appears to reflect the response to drought. Leaf shedding is a strategy to reduce moisture loss in semi-arid environments. Herbaceous species, both annuals and perennials, were strongly related to soil

nutrients (C:N, AP). The availability of phosphorus and organic sources of nitrogen in the soil varies seasonally with soil organic matter turnover, temperature, pH and water availability in the soil (Troeh & Thompson 2005). The abundance of PFTs related to nutrient and water acquisition was significantly related to altitude which was highly correlated with the first RDA axis. Succulents tended to be associated with sand and AP in the soil. They are able to buffer the effect of water shortage in the lower elevation zones (Diaz *et al.* 1999).

Generally, our results show that topographic attributes (altitude and slope) and SOC play an important role in differentiating the relative abundance of PFTs in the landscape. The categorization of PFTs reveals differential response of plants to environmental gradients which structure the vegetation in a landscape. In the future, the inclusion of disturbance regimes such as fire and grazing and PFTs related to them would provide an even better picture of functional patterns of vegetation. Further attempts to characterize PFTs and their response to environmental gradients should include traits related to water harvesting (e.g. rooting depth), degree of ramification, and drought avoidance.

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Electronic Appendix for Manuscript 2: Species and plant functional types

Nomenclature follows the published Flora volumes of Ethiopian and Eritrea (Edwards *et al.* 1995, 1997, 2000; Hedberg & Edwards 1989, 1995; Hedberg *et al.* 2003, 2004)

Abrevations: Cl = Climbers; Rh = Rhizomes/stolons; Nf = Nitrogen fixers; An = Annuals
He = Herbs; Ro = Rosettes; Pa = Parasites; De = Deciduous
Wo = Woody; Th = Thorns/spines; Su = Succulents; Ev = Evergreens
Fe = Ferns; Tu = Tussocks; Pe = Perennials
Gr = Graminoids; Na = No adaptation/do not fit into the specified strategies

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Acanthus eminens C.B.Clarke	Acanthaceae	Wo	Th	Na	Ev
Barleria eranthemoides R. Br. ex C.B.Clarke	Acanthaceae	He	Th	Na	Pe
Barleria grandicalyx Lindau	Acanthaceae	He	Th	Na	Pe
Barleria ventricosa Hochst. ex Nees.	Acanthaceae	He	Th	Na	Pe
Blepharis maderaspatensis (L.) Roth	Acanthaceae	He	Th	Na	Pe
Crabbea velutina S. Moore	Acanthaceae	He	Na	Na	Pe
Dicliptera maculata Nees	Acanthaceae	He	Na	Na	Pe
Hypoestes forskaolii (Vahl) R. Br.	Acanthaceae	He	Na	Na	Pe
Hypoestes triflora (Forssk.) Roem. & Schult.	Acanthaceae	He	Na	Na	Pe
Isoglossa punctata (Vahl) Brumitt & Wood.	Acanthaceae	He	Na	Na	Pe
Isoglossa sp.	Acanthaceae	He	Na	Na	Pe
Justicia bizuneshiae Ensermu	Acanthaceae	He	Na	Na	Pe
Justicia cordata (Nees) T. Anderson	Acanthaceae	He	Na	Na	Pe
Justicia flava (Vahl) Vahl	Acanthaceae	He	Na	Na	Pe
Justicia glabra Koenig ex Roxb.	Acanthaceae	He	Na	Na	Pe
Monechma debile (Forssk.) Nees	Acanthaceae	He	Na	Na	An
Phaulopsis imbricata (Forssk.) Sweet	Acanthaceae	He	Na	Na	Pe
Ruellia patula Jacq.	Acanthaceae	He	Na	Na	Pe
Ruellia prostrata Poir.	Acanthaceae	He	Na	Na	Pe
Thunbergia alata Boj. ex. Sims	Acanthaceae	Cl	Na	Na	Pe
Thunbergia annua Hoshst.	Acanthaceae	Cl	Na	Na	Pe
Aloe sp.	Aloaceae	Wo	Th	Su	Ev
Achyranthes aspera L.	Amaranthaceae	He	Th	Na	Pe
Cyathula cylindrica Moq.	Amaranthaceae	He	Th	Na	Pe
Pupalia grandiflora Peter	Amaranthaceae	He	Na	Na	Pe
Lannea triphylla (A. Rich.) Engl.	Anacardiaceae	Wo	Na	Na	De
Ozoroa insignis Del.	Anacardiaceae	Wo	Na	Na	Ev
Rhus natalensis Krauss	Anacardiaceae	Wo	Na	Na	Ev
Rhus ruspolii Engl.	Anacardiaceae	Wo	Na	Na	De
Sclerocarya birrea (A. Rich.) Hochst.	Anacardiaceae	Wo	Na	Na	De
Agrocharis melanantha Hochst.	Apiaceae	He	Ro	Na	Pe
Alepidea peduncularis Stued. ex A. Rich.	Apiaceae	He	Na	Na	Pe
Centella asiatica (L.) Urban	Apiaceae	He	Na	Na	Pe
Heracleum abyssinicum (Boiss.) Norman	Apiaceae	He	Na	Na	Pe
Heteromorpha arborescens (Spreng.) Cham. & Schlecht.	Apiaceae	Wo	Na	Na	De
Pimpinella oreophila Hook. f.	Apiaceae	He	Na	Na	Pe
Pimpinella schimperi Abebe	Apiaceae	He	Na	Na	Pe
Sanicula elata Buch.-Ham.ex D. Don	Apiaceae	He	Na	Na	An
Torilis arvensis (Hudson) Link	Apiaceae	He	Na	Na	An
Acokanthera schimperi (A.DC.) Schweinf.	Apocynaceae	Wo	Na	Na	Ev
Carissa spinarum L.	Apocynaceae	Wo	Th	Na	Ev
Ilex mitis (L.) Radlk.	Aquifoliaceae	Wo	Na	Na	Ev

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Polyscias fulva (Hiern) Harms	Araliaceae	Wo	Na	Na	Ev
Schefflera abyssinica (Hochst. ex A. Rich.) Harms	Araliaceae	Wo	Na	Na	Ev
Schefflera myriantha (Bak.) Drake	Araliaceae	Wo	Na	Na	Ev
Phoenix reclinata Jacq.	Arecaceae	Wo	Na	Na	Ev
Dregea abyssinica (Hochst.) K. Schum.	Asclepiadaceae	Cl	Na	Na	Pe
Edithcolea grandis N. E. Br.	Asclepiadaceae	He	Na	Su	Pe
Gomphocarpus fruticosus (L.) Ait. f.	Asclepiadaceae	He	Na	Na	Pe
Periploca linearifolia Quert.-Dill. & A. Rich.	Asclepiadaceae	Cl	Na	Na	Pe
Sarcostemma viminale (L.) R. Br.	Asclepiadaceae	Cl	Na	Su	Pe
Secamone parvifolia (Oliv.) Bullock	Asclepiadaceae	Cl	Na	Na	Pe
Tacazzea conferta N. E. Br.	Asclepiadaceae	Cl	Na	Na	Pe
Asparagus africanus Lam.	Asparagaceae	Cl	Th	Na	Pe
Asparagus flagellaries (Kunth) Baker	Asparagaceae	Cl	Th	Na	Pe
Kniphofia isoetifolia Steud. ex. Hochst.	Asphodelaceae	He	Rh	Na	Pe
Asplenium aethiopicum (Burm. f.) Bech.	Aspleniaceae	Fe	Rh	Na	Pe
Asplenium anisophyllum Kze.	Aspleniaceae	Fe	Rh	Na	Pe
Asplenium erectum Willd	Aspleniaceae	Fe	Rh	Na	Pe
Asplenium monanthes L.	Aspleniaceae	Fe	Rh	Na	Pe
Adenostemma mauritianum DC.	Asteraceae	He	Na	Na	An
Ageratum conyzoides L.	Asteraceae	He	Na	Na	An
Aspilia africana (Pers.) C.D. Adams	Asteraceae	He	Na	Na	Pe
Aspilia mossambicensis (Oliv.) Wild	Asteraceae	He	Na	Na	Pe
Bidens pachyloma (Oliv. & Hiern) Cufod.	Asteraceae	He	Na	Na	An
Bidens pilosa L.	Asteraceae	He	Na	Na	An
Bidens ternata (Chiov.) Sherff	Asteraceae	He	Na	Na	Pe
Blumea caffra (DC.) O. Hoffm.	Asteraceae	He	Na	Na	An
Bothriocline schimperi Oliv. & Hiern ex Benth.	Asteraceae	He	Na	Na	Pe
Carduus leptacanthus Fresen.	Asteraceae	He	Th	Na	Pe
Conyza newii Oliv. & Hiern	Asteraceae	Wo	Na	Na	Ev
Conyza pedunculata (Oliv.) Wild.	Asteraceae	He	Na	Na	Pe
Conyza pyrrhopappa Sch.Bip. ex A. Rich.	Asteraceae	Wo	Na	Na	Ev
Conyza sumatrensis (Retz.) E.H. Walker	Asteraceae	He	Na	Na	An
Crassocephalum macropappum (Sch. Bip. ex A. Rich.) S. Moore	Asteraceae	He	Na	Na	Pe
Crepis rueppellii Sch. Bip.	Asteraceae	He	Ro+Rh	Su	Pe
Dichrocephala integrifolia (L.f.) Kuntze	Asteraceae	He	Na	Na	An
Eclipta prostrata (L.) L.	Asteraceae	He	Na	Na	An
Emilia herbaceae Mesfin & Beentje	Asteraceae	He	Na	Na	An
Emilia serpentines Mesfin & Beentje	Asteraceae	He	Na	Na	Pe
Guizotia schimperi Sch. Bip. ex Walp	Asteraceae	He	Na	Na	Pe
Helichrysum argyranthum O.Hoffm.	Asteraceae	He	Na	Na	Pe
Helichrysum foetidum (L.) Moench.	Asteraceae	He	Na	Na	An
Helichrysum formosissimum Sch. Bip. ex A. Rich.	Asteraceae	He	Na	Na	Pe
Helichrysum globosum A. Rich.	Asteraceae	He	Na	Na	Pe
Helichrysum nudifolium (L.) Less.	Asteraceae	He	Na	Na	Pe
Helichrysum schimperi (Sch. Bip ex A.Rich.) Moeser	Asteraceae	He	Na	Na	Pe
Helichrysum traversii Chiov.	Asteraceae	He	Na	Na	Pe
Inula paniculata (Klatt) Burtt-Dary	Asteraceae	He	Ro	Na	Pe
Kleinia squarrosa Cufod.	Asteraceae	Wo	Na	Su	De
Laggera crispata (Vahl) Hepper & Wood	Asteraceae	He	Na	Na	An
Melanthera scandens (Schumach. & Thonn.) Roberty	Asteraceae	Cl	Na	Na	Pe
Microglossa pyrifolia (Lam.) Kuntze	Asteraceae	Wo	Na	Na	Ev
Parthenium hysterophorus L.	Asteraceae	He	Na	Na	Pe
Plectocephalus varians (A. Rich.) C. Jeffrey ex. Cufod.	Asteraceae	He	Rh	Su	Pe
Pluchea dioscoridis (L.) DC.	Asteraceae	He	Na	Na	Pe

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Senecio myriocephalus Sch. Bip. ex A. Rich.	Asteraceae	Wo	Na	Na	Ev
Senecio subsessilis Oliv. & Hiern	Asteraceae	He	Rh	Na	Pe
Sonchus oleraceus L.	Asteraceae	He	Na	Na	An
Spilanthes costata Benth.	Asteraceae	He	Na	Na	An
Vernonia auriculifera Hiern.	Asteraceae	Wo	Na	Na	Ev
Vernonia galamensis (Cass.) Less.	Asteraceae	He	Na	Na	An
Vernonia hymenolepis A. Rich.	Asteraceae	Wo	Na	Na	Ev
Vernonia myriantha Hook. f.	Asteraceae	Wo	Na	Na	Ev
Vernonia popeana C. Jeffrey	Asteraceae	He	Na	Na	Pe
Vernonia urticifolia A. Rich.	Asteraceae	Wo	Na	Na	Ev
Vernonia wollastonii S. Moore	Asteraceae	He	Na	Na	Pe
Xanthium strumarium L.	Asteraceae	He	Th	Na	An
Balanites aegyptiaca (L.) Del.	Balanitaceae	Wo	Th	Na	Ev
Balanites rotindifolia (van Tieghem) Blatter	Balanitaceae	Wo	Th	Na	Ev
Impatiens hochstetteri Warb.	Balsaminaceae	He	Na	Su	An
Impatiens tinctoria A. Rich.	Balsaminaceae	He	Na	Su	Pe
Cordia africana Lam.	Boraginaceae	Wo	Na	Na	De
Cordia ovalis R.Br.	Boraginaceae	Wo	Na	Na	Ev
Cynoglossum amplifolium Hochst. ex A. DC.	Boraginaceae	He	Na	Na	Pe
Ehertia cymosa Thonn.	Boraginaceae	Wo	Na	Na	Ev
Commiphora habessinica (Berg) Engl.	Burseraceae	Wo	Th	Na	De
Lobelia gibberoa Hemsl.	Campanulaceae	Wo	Na	Na	Ev
Monopsis stellarioides (Presl.) Urb.	Campanulaceae	He	Na	Na	An
Wahlenbergia erectum (Roth. ex Roem. & Schult.) Tuyn	Campanulaceae	He	Na	Na	An
Wahlenbergia hirsuta (Edgew.) Tuyn	Campanulaceae	He	Na	Na	An
Boscia salicifolia Oliv.	Capparidaceae	Wo	Na	Na	Ev
Cadaba farinosa Forssk.	Capparidaceae	Wo	Na	Na	Ev
Capparis fascicularis DC.	Capparidaceae	Cl	Th	Na	Ev
Crateva adansonii DC.	Capparidaceae	Wo	Na	Na	Ev
Maerua crassifolia Forssk.	Capparidaceae	Wo	Na	Na	Ev
Cerastium octandrum A. Rich.	Caryophyllaceae	He	Na	Na	An
Polycarpaea eriantha Hochst.	Caryophyllaceae	He	Na	Na	An
Maytenus arbutifolia (A. Rich.) Wilczek	Celastraceae	Wo	Th	Na	De
Maytenus gracilipes (Welw. ex Oliv.) Exell	Celastraceae	Wo	Th	Na	Ev
Maytenus senegalensis (Lam.) Exell	Celastraceae	Wo	Na	Na	Ev
Combretum aculeatum Vent.	Combretaceae	Wo	Na	Na	De
Combretum collinum Fresen.	Combretaceae	Wo	Na	Na	De
Combretum molle R. Br. ex G. Don	Combretaceae	Wo	Na	Na	De
Terminalia brownii Fresen.	Combretaceae	Wo	Na	Na	De
Terminalia schimperiana Hochst.	Combretaceae	Wo	Na	Na	De
Aneilema rendlei C.B. Clarke	Commelinaceae	He	Na	Su	Pe
Commelina africana L.	Commelinaceae	He	Rh	Su	Pe
Commelina benghalensis L.	Commelinaceae	He	Na	Su	An
Commelina diffusa Burm.f.	Commelinaceae	He	Na	Su	An
Commelina reptans Brenan	Commelinaceae	He	Rh	Su	Pe
Cyanotis barbata D. Don	Commelinaceae	He	Rh	Su	Pe
Cyanotis foecunda Hochst. ex. Hassk.	Commelinaceae	He	Rh	Su	Pe
Convolvulus kilimandschari Engl.	Convolvulaceae	Cl	Na	Na	Pe
Evolvulus alsinoides (L.) L.	Convolvulaceae	He	Na	Na	Pe
Ipomoea cairica (L.) Sweet	Convolvulaceae	Cl	Na	Na	Pe
Ipomoea heterotricha F. Didr.	Convolvulaceae	He	Na	Na	An
Ipomoea kituiensis Vtake	Convolvulaceae	Cl	Na	Na	Ev
Ipomoea obscura (L.) Ker-Gawl.	Convolvulaceae	Cl	Na	Na	Pe
Seddera arabica (Forssk.) Choisy	Convolvulaceae	He	Na	Na	Pe

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Crassula alsinoides (Hook.f.) Engl.	Crassulaceae	He	Na	Na	Pe
Kalanchoe glaucescens Britten	Crassulaceae	He	Na	Su	Pe
Kalanchoe lanceolata (Forssk.) Pers.	Crassulaceae	He	Na	Su	An
Kalanchoe petitiana A. Rich.	Crassulaceae	He	Na	Su	Pe
Umbilicus botryoides A. Rich.	Crassulaceae	He	Rh	Su	Pe
Kedrostis foetidissima (Jacq.) Cogn.	Cucurbitaceae	Cl	Na	Na	Pe
Lagenaria abyssinica (Hook.f.) C. Jeffrey	Cucurbitaceae	Cl	irritating hairs	Na	Pe
Zeheneria scabra (Linn. f.) Sond.	Cucurbitaceae	Cl	Rh	Na	Pe
Cupressus lusitanica Miller	Cupressaceae	Wo	Na	Na	Ev
Juniperus procera Hochst. Ex Endl.	Cupressaceae	Wo	Na	Na	Ev
Cyathea sp.	Cyatheaceae	Fe	Rh	Na	Ev
Carex chlorosaccus C.B. Clarke	Cyperaceae	Gr	Ro	Na	Pe
Carex johnstonii Böckl.	Cyperaceae	Gr	Ro	Na	Pe
Cyperus alopecuroides Rottb.	Cyperaceae	Gr	Tus	Na	Pe
Cyperus dubius Rottb.	Cyperaceae	Gr	Rh	Na	Pe
Cyperus alternifolius L	Cyperaceae	Gr	Rh	Na	Pe
Cyperus papyrus L.	Cyperaceae	Gr	Rh	Na	Pe
Cyperus sesquiflorus (Torr.) Mattf. & Kük.	Cyperaceae	Gr	Rh	Na	Pe
Schoenoplectus corymbosus (Roem. & Schult.) Rayn	Cyperaceae	Gr	Rh	Na	Pe
Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae	Fe	Rh	Na	Pe
Dipsacus pinnatifidus Steud. ex A. Rich.	Dipsacaceae	He	Rh	Na	Pe
Pterocephalus frutescens Hochst. ex A. Rich.	Dipsacaceae	He	Na	Na	Pe
Dracaena afromontana Mildbr.	Dracaenaceae	Wo	Na	Na	Ev
Sansevieria ehrenberii Schweinf. ex Baker	Dracaenaceae	He	Rh	Su	Pe
Sansevieria forskoaliana (Shult. f.) Heper & Wood.	Dracaenaceae	He	Rh	Su	Pe
Drynaria volkensii Hiern.	Drynariaceae	Fe	Rh	Na	Pe
Polystichum fuscopaleaceum Alston	Dryopteridaceae	Fe	Rh	Na	Pe
Polystichum transvaalense C.N. Anthony	Dryopteridaceae	Fe	Rh	Na	Pe
Diospyros abyssinica (Hiern) F. White	Ebenaceae	Wo	Na	Na	Ev
Euclea divinorum Hiern	Ebenaceae	Wo	Na	Na	Ev
Agarista salicifolia (Comm. ex Lam.) Hook.f.	Ericaceae	Wo	Na	Na	Ev
Erica arborea L.	Ericaceae	Wo	Na	Na	De
Erica tenuipilosa (Engl. ex Alm & Fries) Cheek	Ericaceae	Wo	Na	Na	Ev
Acalyha fruticosa Forssk.	Euphorbiaceae	He	Na	Na	An
Acalypha crenata A. Rich.	Euphorbiaceae	Wo	Na	Na	Ev
Acalypha villicaulis A. Rich.	Euphorbiaceae	Wo	Na	Na	Ev
Acalypha volkensii Pax	Euphorbiaceae	He	Na	Na	Pe
Clutia abyssinica Jaub. & Spach.	Euphorbiaceae	Wo	Na	Na	Ev
Croton macrostachyus Del.	Euphorbiaceae	Wo	Na	Na	De
Euphorbia ampliphylla Pax	Euphorbiaceae	Wo	Th	Su	Ev
Euphorbia borenensis A. Gilbert	Euphorbiaceae	Wo	Th	Na	Ev
Euphorbia dumalis S.Carter	Euphorbiaceae	Wo	Na	Na	Ev
Euphorbia inaequilatera Sond.	Euphorbiaceae	He	Na	Na	An
Euphorbia polyacantha Pax	Euphorbiaceae	Wo	Th	Na	Ev
Euphorbia schimperiana Scheele	Euphorbiaceae	He	Na	Na	An
Euphorbia sp. 1	Euphorbiaceae	Wo	Th	Na	Ev
Euphorbia sp. 2	Euphorbiaceae	Wo	Th	Su	Ev
Euphorbia tirucalli L.	Euphorbiaceae	Wo	Na	Na	Ev
Flueggea virosa (Willd.) Voigt.	Euphorbiaceae	Wo	Na	Na	De
Phyllanthus maderaspatensis L.	Euphorbiaceae	Wo	Na	Na	Ev
Ricinus communis L.	Euphorbiaceae	He	Na	Na	Pe
Acacia albida Del.	Fabaceae	Wo	Th	Nf	De
Acacia brevispica Harms	Fabaceae	Wo	Th	Nf	De

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Acacia mellifera (Vahl) Benth.	Fabaceae	Wo	Th	Nf	De
Acacia nilotica (L.) Willd. ex Del.	Fabaceae	Wo	Th	Nf	De
Acacia polyacantha Willd.	Fabaceae	Wo	Th	Nf	De
Acacia senegal (L.) Willd.	Fabaceae	Wo	Th	Nf	De
Acacia seyal Del.	Fabaceae	Wo	Th	Nf	De
Acacia tortilis (Forssk.) Hayne	Fabaceae	Wo	Th	Nf	De
Aeschynomene abyssinica (A. Rich.) Vatke	Fabaceae	Wo	Na	Nf	Ev
Aeschynomene elaphroxylon Jaub.	Fabaceae	Wo	Th	Nf	Ev
Albizia gummifera (J.F.Gmel.) C.A.Sm.	Fabaceae	Wo	Na	Nf	Ev
Albizia schimperiana Oliv.	Fabaceae	Wo	Na	Nf	De
Alysicarpus rugosus (Willd.) DC.	Fabaceae	He	Na	Nf	An
Calpurnia aurea (Ait.) Benth.	Fabaceae	Wo	Na	Nf	Ev
Chamaecrista mimosoides (L.) Greene	Fabaceae	He	Na	Nf	An
Clitoria ternatea L.	Fabaceae	Cl	Na	Nf	Pe
Crotalaria agatiflora Schweinf. subsp.enlangeri Bak.f.	Fabaceae	He	Na	Nf	An
Crotalaria cephalotes Steud. A. Rich.	Fabaceae	He	Na	Nf	An
Crotalaria cylindrica A. Rich.	Fabaceae	He	Na	Nf	Pe
Crotalaria gillettii Polhill	Fabaceae	He	Na	Nf	An
Crotalaria laburnifolia L.	Fabaceae	He	Na	Nf	Pe
Desmodium adscendens (Sw.) DC.	Fabaceae	He	Na	Nf	Pe
Desmodium barbatum (L.) Benth.	Fabaceae	He	Na	Nf	Pe
Desmodium repandum (Vahl) DC.	Fabaceae	Cl	Na	Nf	Pe
Desmodium velutinum (Willd.) DC.	Fabaceae	Wo	Na	Nf	Ev
Dichrostachys cinerea (L.) Wight & Arn.	Fabaceae	Wo	Th	Nf	De
Dolichos sericeus E. Mey.	Fabaceae	Cl	Na	Nf	Pe
Entada abyssinica Steud. ex A. Rich.	Fabaceae	Wo	Na	Nf	De
Eriosema robustum Bak.	Fabaceae	Cl	Na	Nf	Pe
Erythrina brucei Schweinf.	Fabaceae	Wo	Th	Nf	De
Glycine wightii (Wight & Arn.) Verdc.	Fabaceae	Cl	Na	Nf	Pe
Indigofera amorphoides Jaub. & Spach	Fabaceae	He	Na	Nf	Pe
Indigofera arrecta Hochst ex A. Rich.	Fabaceae	Wo	Na	Nf	De
Indigofera atriceps Hook. F.	Fabaceae	Wo	Na	Nf	De
Indigofera brevicalyx Bak.f.	Fabaceae	He	Na	Nf	Pe
Indigofera colutea (Burm.f.) Merr.	Fabaceae	He	Na	Nf	An
Indigofera emarginella Steud. ex A. Rich.	Fabaceae	Wo	Na	Nf	Ev
Indigofera garckeana Vatke	Fabaceae	Wo	Na	Nf	Ev
Indigofera spicata Forssk.	Fabaceae	He	Na	Nf	Pe
Macrotyloma axillare (E. Mey.) Verdc.	Fabaceae	Cl	Na	Nf	Pe
Parochaetus communis D. Don	Fabaceae	He	Na	Nf	Pe
Piliostigma thonningii (Schumach.) Milne-Redh.	Fabaceae	Wo	Na	Nf	Ev
Pterolobium stellatum (Forssk.) Brenan	Fabaceae	Wo	Th	Nf	Ev
Rhynchosia densiflora (Roth) DC.	Fabaceae	Cl	Na	Nf	Pe
Rhynchosia minima (L.) DC.	Fabaceae	Cl	Na	Nf	Pe
Rhynchosia resinosa (Hochst. ex A. Rich.) Bak.	Fabaceae	Cl	Na	Nf	Ev
Senna obtusifolia (L.) Irwin & Barneby	Fabaceae	Wo	Na	Na	Ev
Sesbania sesban (L.) Merr.	Fabaceae	Wo	Na	Nf	Ev
Tephrosia elata Deflers	Fabaceae	Wo	Na	Nf	Ev
Tephrosia emeroides A. Rich.	Fabaceae	Wo	Na	Nf	Ev
Tephrosia interrupta Hochst. & Steud. ex Engl.	Fabaceae	Wo	Na	Nf	Ev
Tephrosia linearis (Willd.) Pers.	Fabaceae	Wo	Na	Nf	Ev
Tephrosia pentaphylla (Roxb.) G. Don	Fabaceae	Wo	Na	Nf	Ev
Tephrosia villosa (L.) Pers.	Fabaceae	Wo	Na	Nf	Ev
Trifolium simense Fresen.	Fabaceae	He	Na	Nf	Pe
Vigna membranacea A. Rich.	Fabaceae	Cl	Na	Nf	Pe

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Vigna parkeri Bak.	Fabaceae	Cl	Na	Nf	Pe
Dovyalis abyssinica (A. Rich) Warb.	Flacourtiaceae	Wo	Th	Na	Ev
Flacourtia indica (Burm.f.) Merr.	Flacourtiaceae	Wo	Th	Na	De
Sebaea brachyphylla Griseb.	Gentianaceae	He	Na	Na	An
Swertia abyssinica Hochst.	Gentianaceae	He	Ro	Na	An
Swertia lugardae Bullock	Gentianaceae	He	Ro	Na	An
Geranium sp.	Geraniaceae	He	Na	Na	Pe
Pelargonium glechomoides Hochst.	Geraniaceae	He	Na	Na	Pe
Apodytes dimidiata E. Mey. ex Arn.	Icacinaceae	He	Na	Na	An
Hypericum quartinianum A. Rich.	Hypericaceae	Wo	Na	Na	Ev
Hypericum revolutum Vahl	Hypericaceae	Wo	Na	Na	Ev
Trichocladus ellipticus Eckl. & Zeyh.	Hamamelidaceae	Wo	Na	Na	Ev
Aristea abyssinica Pax	Iridaceae	Wo	Na	Na	Ev
Achyrospermum schimperi (Hochst. ex Briq.) Perkins	Lamiaceae	He	Na	Na	Pe
Ajuga integrifolia Buch.-Ham. ex D.Don	Lamiaceae	He	Na	Na	Pe
Becium filamentosum (Forssk.) Chiov.	Lamiaceae	He	Na	Na	Pe
Clerodendron myricoides (Hochst.) R. Br.ex Vatke.	Lamiaceae	He	Na	Na	Pe
Hoslundia opposita Vahl	Lamiaceae	Wo	Na	Na	De
Leonotis ocymifolia (Burm.f.) Iwarsson	Lamiaceae	Wo	Na	Na	Ev
Leucas glabrata (Vahl) R.Br.	Lamiaceae	He	Na	Na	Pe
Leucas martinicensis (Jacq.) R. Br.	Lamiaceae	He	Na	Na	An
Leucaus abyssinica (Benth.) Briq.	Lamiaceae	He	Na	Na	An
Ocimum lamiifolium (Hochst. ex Bent.) DC.	Lamiaceae	Wo	Na	Na	Ev
Platostoma rotundifolium (Briq.) A.J. Paton	Lamiaceae	He	Na	Na	Pe
Plectranthus barbatus Andr.	Lamiaceae	He	Na	Na	Pe
Plectranthus cylindraceus Hochst. ex Benth.	Lamiaceae	He	Rh	Su	Pe
Plectranthus lanuginosus (Hochst. ex. Benth.) Agnew	Lamiaceae	He	Rh	Su	Pe
Plectranthus minutiflorus Ryding	Lamiaceae	He	Rh	Su	Pe
Plectranthus rupestris (Hochst.) Baker	Lamiaceae	He	Rh	Su	Pe
Premna schimperi Engl.	Lamiaceae	Wo	Na	Na	Ev
*Pycnostachys abyssini*ca Fresen.	Lamiaceae	He	Rh	Su	Pe
Pycnostachys eminii Gürke	Lamiaceae	He	Na	Na	Ev
Pycnostachys meyeri Gürke	Lamiaceae	Wo	Na	Na	Ev
Satureja abyssinica (Benth.) Briq.	Lamiaceae	Wo	Na	Na	Ev
Satureja paradoxa (Vatke) Engl.	Lamiaceae	He	Na	Na	An
Satureja pseudosimensis Brenan	Lamiaceae	He	Na	Na	Pe
Satureja punctata (Benth.) Briq.	Lamiaceae	He	Na	Na	Pe
Stachys aculeolata Hook. f.	Lamiaceae	He	Na	Na	Pe
Cassytha filiformis L.	Lauraceae	He	Na	Na	An
Buddleja polystachya Fresen.	Buddlejaceae	Wo	Na	Pa	Ev
Nuxia congesta R.Br. ex Fresen.	Buddlejaceae	Wo	Na	Na	Ev
Englerina woodfordioides (Schweinf.) M. Gilbert	Loranthaceae	Wo	Na	Na	Ev
Erianthemum dregei (Eckl. & Zeyh.) Tieghem	Loranthaceae	Fe	Rh	Na	Pe
Oncocalyx glabratus (Engl.) M. Gilbert	Loranthaceae	Wo	Na	Pa	Pe
Tapianthus globiferus (A. Rich.) Tieghem	Loranthaceae	Wo	Na	Pa	Pe
Tapianthus heteromorphus (A. Rich.)	Loranthaceae	Wo	Na	Pa	Ev
Huperzia dacrydioides (Baker) Pic. Serm.	Lycopodiaceae	Epiphyte	Na	Pa	Ev
Abutilon bidentatum (Hochst.) A. Rich.	Malvaceae	Wo	Na	Pa	Ev
Abutilon fruticosum Guill. & Perr.	Malvaceae	Wo	Na	Na	Pe
Hibiscus machranthus Hochst. ex A. Rich.	Malvaceae	He	Na	Na	Pe
Hibiscus micranthus L.f.	Malvaceae	He	Na	Na	Pe
Kosteletzkya adoensis (Hochst. ex. A. Rich.) Mast.	Malvaceae	Wo	irritating hairs	Na	Ev
Sida ovata Forssk.	Malvaceae	Wo	Na	Na	Ev

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Eckebergia capensis Saprrm	Meliaceae	He	Na	Na	Pe
Lepidotrichilia volkensii (Gürke) Leroy	Meliaceae	He	Na	Na	Pe
Bersama abyssinica Fresen.	Melianthaceae	Wo	Na	Na	Ev
Stephania abyssinica (Dillion ex A. Rich.) Walp.	Menispermaceae	Wo	Na	Na	Ev
Corbichonia decumbens (Forssk.) Exell	Molluginaceae	Wo	Na	Na	Ev
Mollugo nudicaulis Lam.	Molluginaceae	Cl	Na	Na	Pe
Dorestenia soerensenii Friis	Moraceae	He	Na	Na	An
Ficus sur Forssk.	Moraceae	He	Ro	Na	An
Ficus sycomorus L.	Moraceae	He	Rh	Na	Pe
Ficus vasta Forssk.	Moraceae	Wo	Na	Na	De
Embelia schimperi Vatke	Myrsinaceae	Wo	Na	Na	De
Maesa lanceolata Forssk.	Myrsinaceae	Wo	Na	Na	De
Myrsine africana L.	Myrsinaceae	Wo	Na	Na	Ev
Myrsine melanophloeos (L.) R. Br.	Myrsinaceae	Wo	Na	Na	Ev
Syzygium guineense (Willd.) DC. ssp. afromontanum F. White	Myrtaceae	Wo	Na	Na	Ev
Ochna insermis (Forssk.) Schweinf. ex Penzig	Ochnaceae	Wo	Na	Na	Ev
Ximenia americana L.	Olacaceae	Wo	Na	Na	Ev
Jasminum abyssinicum Hochst. ex DC.	Oleaceae	Wo	Na	Na	Ev
Jasminum grandiflorum L.	Oleaceae	Wo	Th	Na	Ev
Olea europea L. ssp. cuspidata (Wall. ex G. Don) Cif.	Oleaceae	Cl	Na	Na	Ev
Schrebera alata (Hochst.) Welw.	Oleaceae	Cl	Na	Na	Ev
Arthropteris monocarpa (Cordem.) C. Chr.	Oleandraceae	Wo	Na	Na	Ev
Arthropteris orientalis (J.F.Gmel.) Posth.	Oleandraceae	Wo	Na	Na	Ev
Olinia rochetiana A. Juss.	Oliniaceae	Fe	Rh	Na	Pe
Diaphananthe schimperiana (A. Rich.) Summerh.	Orchidaceae	Fe	Rh	Na	Pe
Oxalis corniculata L.	Oxalidaceae	Wo	Na	Na	Ev
Phytolacca dodecandra L´Herit.	Phytolaccaceae	He	Rh	Su	Pe
Peperomia abyssinica Miq.	Piperaceae	He	Na	Na	An
Piper capense L.f.	Piperaceae	He	Na	Na	Pe
Pittosporum abyssinica Del.	Pittosporaceae	He	Na	Su	Pe
Pittosporum viridiflorum Sims	Pittosporaceae	He	Rh	Na	Pe
Plantago palmata Hook. F.	Plantaginaceae	Wo	Na	Na	Ev
Andropogon abyssinicus Fresen.	Poaceae	Wo	Na	Na	Ev
Aristida adscensionis L.	Poaceae	He	Ro	Na	Pe
Arthraxon micans (Nees) Hochst.	Poaceae	Gr	Na	Na	An
Arundinaria alpina K. Schum.	Poaceae	Gr	Na	Na	An
Bothriochloa insculpta (Hochst. ex A. Rich.) A. Camus	Poaceae	Gr	Rh	Na	An
Brachiaria leersioides (Hochst.) Stapf	Poaceae	Gr	Rh	Na	Pe
Brachiaria serrata (Thunb.) Stapf	Poaceae	Gr	Tus	Na	Pe
Cenchrus ciliaris L.	Poaceae	Gr	Na	Na	An
Chrysopogon plumulosus Hochst.	Poaceae	Gr	Tus	Na	Pe
Cynodon dactylon (L.) Pers.	Poaceae	Gr	Rh	Na	Pe
Digitaria velutina (Forssk.) P. Beauv.	Poaceae	Gr	Tus	Na	Pe
Echinochloa pyramidalis (Lam.) Hitchc. & Chase	Poaceae	Gr	Na	Na	Pe
Enteropogon machrostachyus Hochst. ex A. Rich. Benth.	Poaceae	Gr	Na	Na	An
Eragrostis cilianensis (All.) Vign. ex Janchen	Poaceae	Gr	Rh	Na	Pe
Exotheca abyssinica (Hochst ex A. Rich.) Anderss.	Poaceae	Gr	Na	Na	Pe
Harpachne schimperi Hochst. ex A. Rich	Poaceae	Gr	Na	Na	An
Heteropogon contortus (L.) Roem. & Schult.	Poaceae	Gr	Tus	Na	Pe
Hyparrhenia filipendula (Hochst.) Stapf	Poaceae	Gr	Rh	Na	Pe
Hyparrhenia hirta (L.) Stapf	Poaceae	Gr	Tus	Na	Pe
Leptochloa obtusiflora Hochst.	Poaceae	Gr	Tus	Na	Pe
Loudetia arundinacea (Hochst. ex A. Rich) Steud.	Poaceae	Gr	Tus	Na	Pe
Melinus repens (Willd.) Zizka	Poaceae	Gr	Na	Na	Pe

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Oplismenus undulatifolius (Ard.) Roem. & Schult.	Poaceae	Gr	Tus	Na	Pe
Panicum atrosanquineum A. Rich.	Poaceae	Gr	Tus	Na	An
Panicum coloratum L.	Poaceae	Gr	Rh	Na	Pe
Panicum hochstetteri Stued.	Poaceae	Gr	Na	Na	An
Panicum maximum Jacq.	Poaceae	Gr	Rh	Na	Pe
Panicum subalbidum Kunth	Poaceae	Gr	Rh	Na	Pe
Perotis patens Gand.	Poaceae	Gr	Rh	Na	Pe
Setaria incrassata (Hochst.) Hack.	Poaceae	Gr	Na	Na	An
Setaria pumila (Poir.) Roem. & Schult.	Poaceae	Gr	Rh	Na	An
Setaria verticillata (L.) P. Beauv.	Poaceae	Gr	Tus	Na	Pe
Sporoboulus piliferus (Trin.) Kunth	Poaceae	Gr	Na	Na	An
Themeda triandra Forssk.	Poaceae	Gr	Na	Na	An
Polygala albida Schinz	Polygalaceae	Gr	Na	Na	An
Polygala arenaria Willd.	Polygalaceae	Gr	Tus	Na	Pe
Polygala erioptera DC.	Polygalaceae	He	Na	Na	An
Polygala rupicola A. Rich.	Polygalaceae	He	Na	Na	An
Polygala sadebeckiana Gürke	Polygalaceae	He	Na	Na	An
Polygala sphenoptera Fresen.	Polygalaceae	He	Na	Na	Pe
Polygonum afromontanium Greenway	Polygonaceae	He	Rh	Na	Pe
Loxogramme lanceolata (Sw.) S. Presl.	Polypodiaceae	He	Na	Na	An
Pleopeltis macrocarpa (Bory ex. Willd) Kaulf	Polypodiaceae	Cl	Na	Na	Ev
Portulaca oleraceae L.	Portulacaceae	Fe	Rh	Na	Pe
Portulaca quadrifida L.	Portulacaceae	Fe	Rh	Na	Pe
Talinum portulacifolium (Forssk.) Achers. ex Schweinf.	Portulacaceae	He	Na	Su	An
Faurea speciosa Welw.	Proteaceae	He	Na	Na	An
Adiantum sp.	Pteridaceae	He	Na	Su	Pe
Pteris catoptera Kze.	Pteridaceae	Wo	Na	Na	Ev
Pteris cretica L.	Pteridaceae	Fe	Na	Na	Pe
Clematis simensis Fresen.	Ranunculaceae	Fe	Rh	Na	Pe
Thalictrum rhynchocarpum Dill. & A. Rich.	Ranunculaceae	Fe	Rh	Na	Pe
Helinus mystacinus (Ait.) E. Mey. ex Steud.	Rhamnaceae	Cl	Na	Na	Ev
Rhamnus prinoides L`Herit.	Rhamnaceae	He	Na	Na	Pe
Rhamnus staddo A. Rich.	Rhamnaceae	Cl	Na	Na	Ev
Ziziphus mucronata Willd.	Rhamnaceae	Wo	Na	Na	Ev
Alchemilla fischeri Engl.	Rosaceae	Wo	Na	Na	Ev
Hagenia abyssinica (Bruce) J.F. Gmel.	Rosaceae	Wo	Th	Na	Ev
Prunus africana (Hook.f.) Kalkm.	Rosaceae	He	Ro	Na	An
Rubus apetalus Poir.	Rosaceae	Wo	Na	Na	Ev
Rubus steudneri Schweinf.	Rosaceae	Wo	Na	Na	Ev
Anthospermum herbaceum L.f.	Rubiaceae	Cl	Th	Na	Ev
Canthium oligocarpum Hiern	Rubiaceae	Cl	Th	Na	Ev
Canthium pseudosetiflorum Bridson	Rubiaceae	He	Na	Na	Pe
Galiniera saxifrage (Hochst.) Bridson	Rubiaceae	Wo	Th	Na	Ev
Galium simense Fresen.	Rubiaceae	Wo	Na	Na	Ev
Galium thunbergianum Eckl. & Zeyh.	Rubiaceae	Wo	Na	Na	Ev
Gardenia ternifolia Schumach. & Thonn.	Rubiaceae	He	Na	Na	Pe
Oldenlandia monanthos (A. Rich.) Hiern	Rubiaceae	He	Rh	Na	Pe
Pavetta oliveriana Hiern	Rubiaceae	Wo	Na	Na	Ev
Pentanisia ouranogyne S. Moore	Rubiaceae	He	Na	Na	Pe
Pentas lanceolata (Forssk.) Deflers	Rubiaceae	Wo	Na	Na	Ev
Pentas schimperana (A. Rich.) Vtake	Rubiaceae	He	Na	Na	Pe
Psychotria orophila Petit	Rubiaceae	He	Na	Na	Pe
Psydrax parviflora (Afz.) Bridson	Rubiaceae	Wo	Na	Na	Ev
Psydrax schimperiana (A. Rich.) Bridson	Rubiaceae	Wo	Na	Na	Ev

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Clausena anisata (Willd.) Benth.	Rutaceae	Wo	Na	Na	Ev
Teclea nobilis Del.	Rutaceae	Wo	Na	Na	Ev
Zanthoxylum chalybeum Engl.	Rutaceae	Wo	Na	Na	Ev
Dobera glabra (Forssk.) Poir.	Salvadoraceae	Wo	Na	Na	Ev
Salvadora persica L.	Salvadoraceae	Wo	Th	Na	De
Osyridocarpus schimperanus (A. Rich.) A. DC.	Santalaceae	Wo	Na	Na	Ev
Osyris quadripartita Decn.	Santalaceae	Wo	Na	Na	Ev
Allophyllus abyssinicus (Hochst.) Radlkofer	Sapindaceae	Cl	Na	Na	Ev
Dodonae angustifolia L.f.	Sapindaceae	Wo	Na	Na	Ev
Lepisanthes senegalensis (Juss. ex Poir.) Leenh.	Sapindaceae	Wo	Na	Na	Ev
Pappea capensis Eckl. & Zeyh.	Sapindaceae	Wo	Na	Na	Ev
Anemia schimperiana Presl	Schizaeaceae	Wo	Na	Na	Ev
Alectra sessiliflora (Vahl) Kuntze	Scrophulariaceae	Wo	Na	Na	Ev
Craterostigma pumilum Hochst.	Scrophulariaceae	Fe	Rh	Na	Pe
Cycnium erectum Randle	Scrophulariaceae	He	Na	Pa	An
Verbascum benthamianum Hepper	scrophulariaceae	He	Ro+Rh	Na	Pe
Veronica abyssinica Fresen.	Scrophulariaceae	He	Na	Na	Pe
Selaginella abyssinica Spring	Selaginaceae	He	Na	Na	Pe
Brucea antidysenterica J.F. Mill.	Simaroubaceae	He	Na	Na	Pe
Harrisonia abyssinica Oliv.	Simaroubaceae	Fe	Na	Na	An
Pellaea viridis (Forssk.) Prantl.	Sinopteriaceae	Wo	Na	Na	Ev
Discopodium penninervium Hochst.	Solanaceae	Wo	Th	Na	Ev
Solanum anguivi Lam.	Solanaceae	Fe	Rh	Na	Pe
Solanum incanum L.	Solanaceae	Wo	Na	Na	Ev
Dombya torrida (J.F. Gmel.) P. Bamps	Sterculiaceae	Wo	Th	Na	Ev
Hermannia tigreensis Hochst. ex A. Rich.	Sterculiaceae	Wo	Th	Na	Ev
Melhania velutina Forssk.	Sterculiaceae	Wo	Na	Na	Ev
Gnidia involucrata Steud. ex A. Rich.	Thymelaeaceae	He	Na	Na	An
Gnidia latifolia (Oliv.) Gilg	Thymelaeaceae	He	Na	Na	Pe
Corchorus trilocularis L.	Tiliaceae	Wo	Na	Na	Ev
Grewia bicolor Juss.	Tiliaceae	Wo	Na	Na	Ev
Grewia velutina (Forssk.) Vahl	Tiliaceae	He	Na	Na	An
Grewia villosa Willd.	Tiliaceae	Wo	Na	Na	Ev
Triumfetta brachyceras K. Schum.	Tiliaceae	Wo	Na	Na	Ev
Triumfetta pilosa Roth	Tiliaceae	Wo	Na	Na	Ev
Triumfetta tomentosa Boj.	Tiliaceae	Wo	Na	Na	Ev
Pilea rivularis Wedd.	Urticaceae	Cl	Na	Na	Pe
Pilea tetraphylla (Steudel) Blume	Urticaceae	Wo	Na	Na	Ev
Urerea hypselodendron (A. Rich.) Wedd.	Urticaceae	He	Rh	Na	Pe
Urtica simensis Steudel	Urticaceae	He	Na	Na	An
Lantana viburnoides (Forssk.) Vahl	Verbenaceae	Cl	Na	Na	Ev
Lippia adoensis Hochst. ex Walp.	Verbenaceae	He	Rh	Na	Pe
Phyla nodiflora (L.) Greene	Verbenaceae	Wo	Th	Na	Ev
Hybanthus enneaspermus (L.) F. Muell.	Violaceae	He	Na	Na	Pe
Viola abyssinica Oliv.	Violaceae	Wo	Na	Na	Ev
Cissus quadrangularis L.	Vitaceae	He	Na	Na	An
Cissus rotundifolia (Forssk.) Vahl	Vitaceae	He	Na	Na	Pe
Cyphostemma adenocaule (Stued. ex A. Rich.) Desc.oings ex Wild & R.B. Drumm.ond.	Vitaceae	Cl	Na	Su	Pe
Cyphostemma cyphoetalum (Fresen.) Desc. ex Wild & R.B. Drumm.Descoings ex Wild & Drummond	Vitaceae	Cl	Na	Su	Pe
Cyphostemma rivae (Gilg) Desc.oings	Vitaceae	Cl	Rh	Na	Pe
Rhoicissus revoilii Planch.	Vitaceae	Cl	Na	Su	Pe
Rhoicissus tridentata (L. f.) Wild & R.B. Drumm.Willd & Drummond	Vitaceae	Cl	Na	Su	Pe
Rhoicissus revoilii Planch.	Vitaceae	Cl	Na	Na	Ev

Species	Families	Growth forms	Stress/ grazing	Water/ nutrient	Temporal attributes
Rhoicissus tridentata (L. f.) Willd & Drummond	Vitaceae	Cl	Na	Na	Ev

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Land use/land cover change in the south-western Ethiopian highlands

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Abstract

Over millennia the Ethiopian highlands have experienced drastic land use/land cover changes due to socio-economic and unsustainable resource use. Yet there have been few studies, which attempted to quantify the pattern and magnitude of land use/land cover changes (LULCC) in the southern Rift Valley and adjacent Ethiopian highlands. This study attempts to answer the following questions: What are the rates and magnitudes of land use/land cover change in the study area? Do highland and Rift Valley sections of the study area show differential trajectories of land use/land cover change? What are the main driving forces for LULCC in the study area? Landsat Multi-Spectral Scanner (MSS), Landsat Thematic Mapper and Enhanced Thematic Mapper plus (ETM+) from the years 1976, 1986 and 2000, respectively were acquired and processed for maximum likelihood classification to generate land use/ land cover maps. Croplands increased from 29 % to 38 % between 1976 and 2000 while bush/ shrubland increased from ~2 % to 12 % over the same period. Conversely, deciduous woodland and sparsely vegetated land cover classes lost an area of about 50 % from 1976 to 2000. Grassland cover increased over the period 1976 to 1986 and then decreased from 1986 to 2000. However, LULCC took differential trajectories over space and time. The highlands were dominantly characterized by land use change to cropland; whereas, the Rift Valley was dominated by land use changes and the transformation of land use/land cover types. After the mid 1980s, however, most land cover classes lost a significant proportion of land to cropland. These changes have potential consequences on local human livelihoods, biodiversity loss and regional environmental change.

Keywords: land cover transitions, land degradation, Rift Valley, Ethiopia

Introduction

Land use/land cover change is the main contributor to global environmental change such as greenhouse gas emissions, the earth's reflectivity (temperature) and water cycles including local and regional precipitation regimes (Geist 2006). It also has a negative consequence on the provision of ecosystem services through watershed degradation, soil erosion and sedimentations (Jones et al. 2001). Land use changes are modifying and fragmenting habitats, increasing the vulnerability of ecosystems to invasive species (Foley et al. 2005; Carpenter et al. 2007), and have persistent legacies in shaping and maintaining ecosystem structures and functions (Foster et al. 2003). Moreover, It was considered as one of the most important drivers of tropical biodiversity loss by the year 2100 (Sala et al. 2000).

LULCC are global phenomena that pose a great challenge, with the rate of change and pattern of transformation varying across spatial and temporal scales (Meyer & Turner 1996). In the developed northern hemisphere, forest cover loss is significantly low with croplands that shrink over time (Lambin et al. 2003), while in most developing countries of the tropics deforestation proceeds at massive scales mainly for the cultivation of crops and pastureland (Meyer & Turner 1996).

Human population growth and density, socio-economic conditions (e.g. poverty) and government policies were important causes for the LULCC in Ethiopia (Zeleke 2000; Gessesse & Kleman 2007; Gessesse & Christiansson 2008). Population growth can limit the capacity of the resource base to supply ecosystem goods such as food (Fairhead et al. 1996) and push the rural poor into marginal lands (Reid et al. 2000). With the human population increasing, the demand for cropland, fuelwood, timber and other resources increase and leads to a process of environmental degradation. Environmental degradation in turn leads to poverty and that again reinforces the process of degradation (Zeleke 2000). A number of

studies (Hurni 1988; McCann 1995; Zeleke 2000) reported severe problems from LULCC as a result of population growth and density, and resultant poverty in the Ethiopian highlands.

The expansion of mechanized agriculture to produce cash crops for export, infrastructure development and lack of tenure security had a great influence especially on regions of the Ethiopian Rift Valley (Gebre 2001; Gessesse & Kleman 2007; Gessesse & Christiansson 2008). The Rift Valley was recognized as the corridor of future development since the 1960s (Gebre 2001) and hence have experienced drastic LULCC. Nevertheless there were very few studies (Gessesse & Kleman 2007; Gessesse & Christiansson 2008) which provide information on the rate and magnitude of land use/land cover dynamics in the southern half of the Rift Valley and the adjacent Ethiopian highlands. This study attempts to answer the following questions: What are the rates and magnitudes of land use/land cover change in the study area? Do highland and Rift Valley sections of the study area show differential trajectories of land use/land cover change? What are the main driving forces for LULCC in the study area?

Materials and methods

The Study Area

The study area is located at $5^{o}42'$ N to 6^{o} 20' N and 37^{o} 17 'E to 37^{o} 59' E (Figure 1). The highest point is in the Gughe highlands peaking at 3546 m a.s.l. (EMA 1994). It serves as a watershed for the inland drainage basin to Lakes Abaya and Chamo in the South- east and the Omo River in the North-west, respectively (Desissa 2007). The physiography of the investigated area is characterized by great diversity, including plateaus, escarpments, horsts, undulating plains, and a graben where Lakes Abaya and Chamo, are located. The lakes have shown fluctuations in the last 50 years and the level of L. Abaya has continuously increased since 1987 due to climatic variability and land use changes (Shütt et al. 2005). The eastern boarder is marked by the Amaro horst, a block mountain that emerged during the formation of the Rift Valley with a peak of 3380 m.s.l. (EMA 1994).

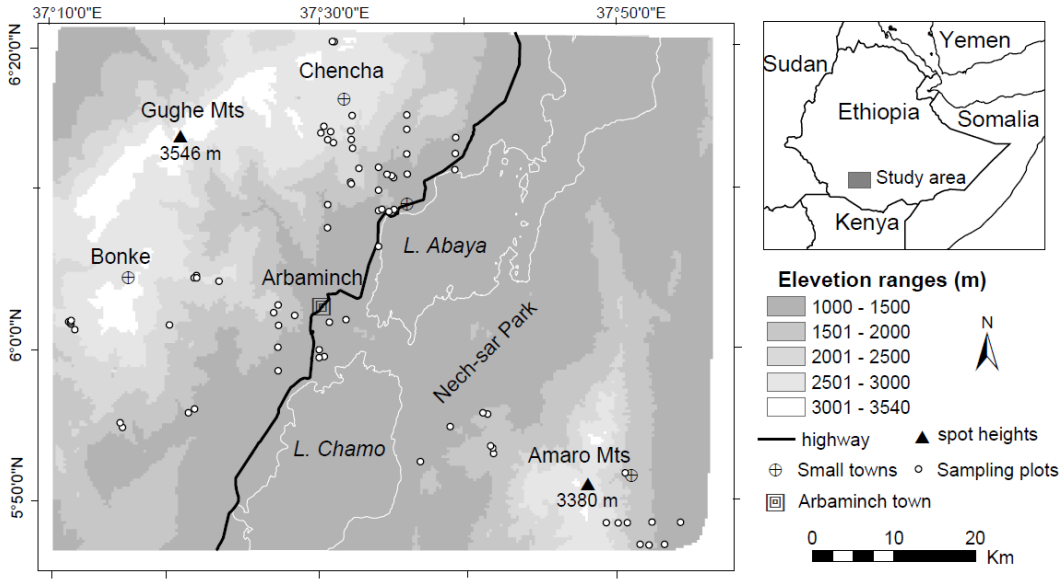

Figure 1 Location map of the study area

Arbaminch (1200 m a.s.l.) has a mean annual temperature of 23° C over the last three decades while Chencha (2700 m.a.s.l.) has a mean annual temperature of 14° C (Figure 2). A bimodal rainfall distribution prevails in the two meteorological stations (Figure 2). The total mean annual rainfall recorded over the last two decades for the two stations, Arbaminch and Chencha, was 888 mm and 1235 mm, respectively. The main rainy season occurs in April and May while the small rainy season is in September and October. Arbaminch experiences a pronounced dry season and consequently has a water shortage for several months of the year (Figure 2a). The Chencha Highlands receive a great deal of rainfall and enjoy a water surplus continuously for several months from February to October (Figure 2b).

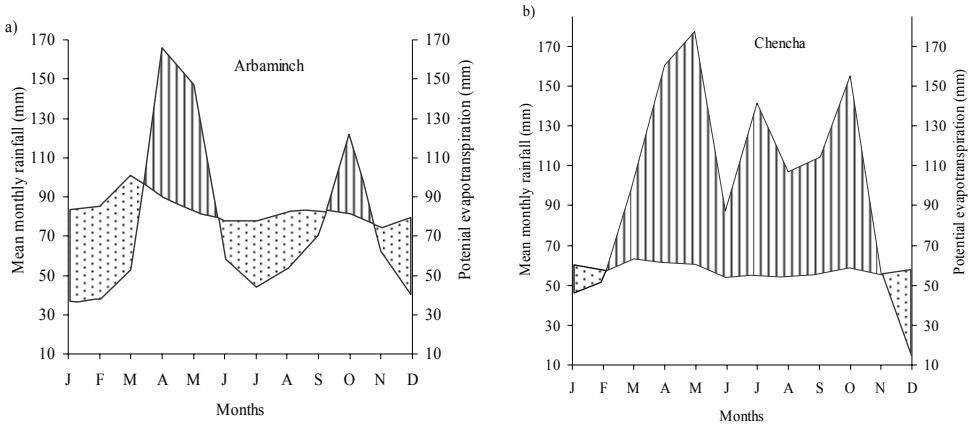

Figure 2 Climate diagram of Arbaminch (a) and Chencha (b) after Thornthwaite (vertical hatching indicate surplus while dot pattern indicate deficit). Arbaminch lies at 1200 m, mean annual temperature = 23°C, total Annual rainfall= 888 mm recorded. Chencha station is located at 2700 m, mean annual temperature = 14°C, total annual rainfall = 1235 mm, PET stands for potential evapo-transpiration. Arbaminch station had a temperature record from 1976 to 2005 and rainfall record from 1987 to 2005. Chencha had a temperature record from 1972 to 1981 while rainfall recorded from 1972 to 2004. However, rainfall records were not continuous and data were missing for Chencha from 1981-1989. All climate records were obtained from the Ethiopian National Meteorological Services Agency (NMSA).

The vegetation of the study area lies within the Somali-Masai regional centre of endemism (White 1983) comprising deciduous woodland, savannah grassland, bush land, and dense thickets, while in the Gughe and Amaro mountains broad-leaved afro-montane rainforests are the dominant climax vegetation (Friis 1992). The Nech-Sar National Park was established in 1972 to conserve the endemic Swayne's Hartebeest and the scenic landscapes of the area and thereby generate economic benefits to the country through the provision of tourism.

Methods

Prior to analysis Landsat images were geo-referenced to the Universal Transverse Mercator (UTM) geographic projection, using Clarke 1880 spheroid, datum Adindan (Ethiopia) and zone 37 N. The Landsat Multi-Spectral Scanner (MSS), the Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper plus (ETM+) were used for the periods 1976, 1986 and 2000, respectively. The Landsat MSS had a coarse resolution of 80 m while the Landsat TM and ETM+ have a resolution of 30 m. Landsat TM and ETM+ were then resampled into 80m to match the spatial resolution to the Landsat Multi-Specteral Scanner. Satellite data were freely obtained from the GLCF website (http://glcf.umiacs.umd.edu/index.shtml).

LULCC analyses were performed with ERDAS imagine 8.5. A supervised maximum likelihood classification method was used to identify land use/land cover types. We have scanned eight topographic-sheet maps (0537A2, B1, B2, 0637C1-C2, C4 and 0636D3, D4), which cover the study area, with a resolution of 600 dots per inch. Then the files were saved in Tag Image Format (TIFF) and georeferenced to Clark 1880, datum Adindan UTM zone 37 N and converted to image format. The topographic sheet maps were obtained from Ethiopian Mapping Agency. We have identified closed patches of forests in the highlands, woodlands and croplands from theses maps as a ground validation for image analysis of the 1976 MSS image and TM of 1986. Regarding the Enhanced Thematic Mapper plus (ETM+), we have made floristic survey of our study area during Novermber-January in 2006/07 and December 2007. These periods match the image acquisitions dates in dry season except for ETM+ (path/row: 1689 -56) in the right bottom corner of the mosaic image (Figure 3a), which was acquired during May 5, 2000. Floristic data were collected from 74 sample points from several categories of woodland, grassland and forests and were used as ground reference points for the classification. However, some classes, which have very close spectral signatures, were combined to reduce errors. For instance, it was not possible to distinguish mountain pasture from cropland. Similarly, degraded Afro-montane forest and bamboo patches were merged into the cover class ‘evergreen forest’. After classification, we compared the three time series of land cover/land use maps to generate a change matrix.

Results

The landscape in the Gughe-Amaro Mountains was largely dominated by cropland, deciduous woodland and wooded grassland over the specified periods (Table 2; Figure 3b). These three categories, without counting the two lakes, covered above 55 percent of the study area (Table 2). Changes in land use/land cover types across the entire region from 1976 to 2000 were significantly large. Bush/shrub woodland and cropland (including mechanized farming) increased in area over the three reference periods (Table 2). Bush/shrub woodland increased tremendously from 100 km² (1.8 %) in 1976 to 669 km² (12.0 %) in 2000 (Table 2). Most of the other land use/land cover types showed a negative change, however. Deciduous woodland and sparsely vegetated land cover classes lost half of their area over two and a half decades

while fire-dominated bushland vegetation declined from 4 % of the total area cover in 1976 to a mere 1% in the year 2000 (Table 2).

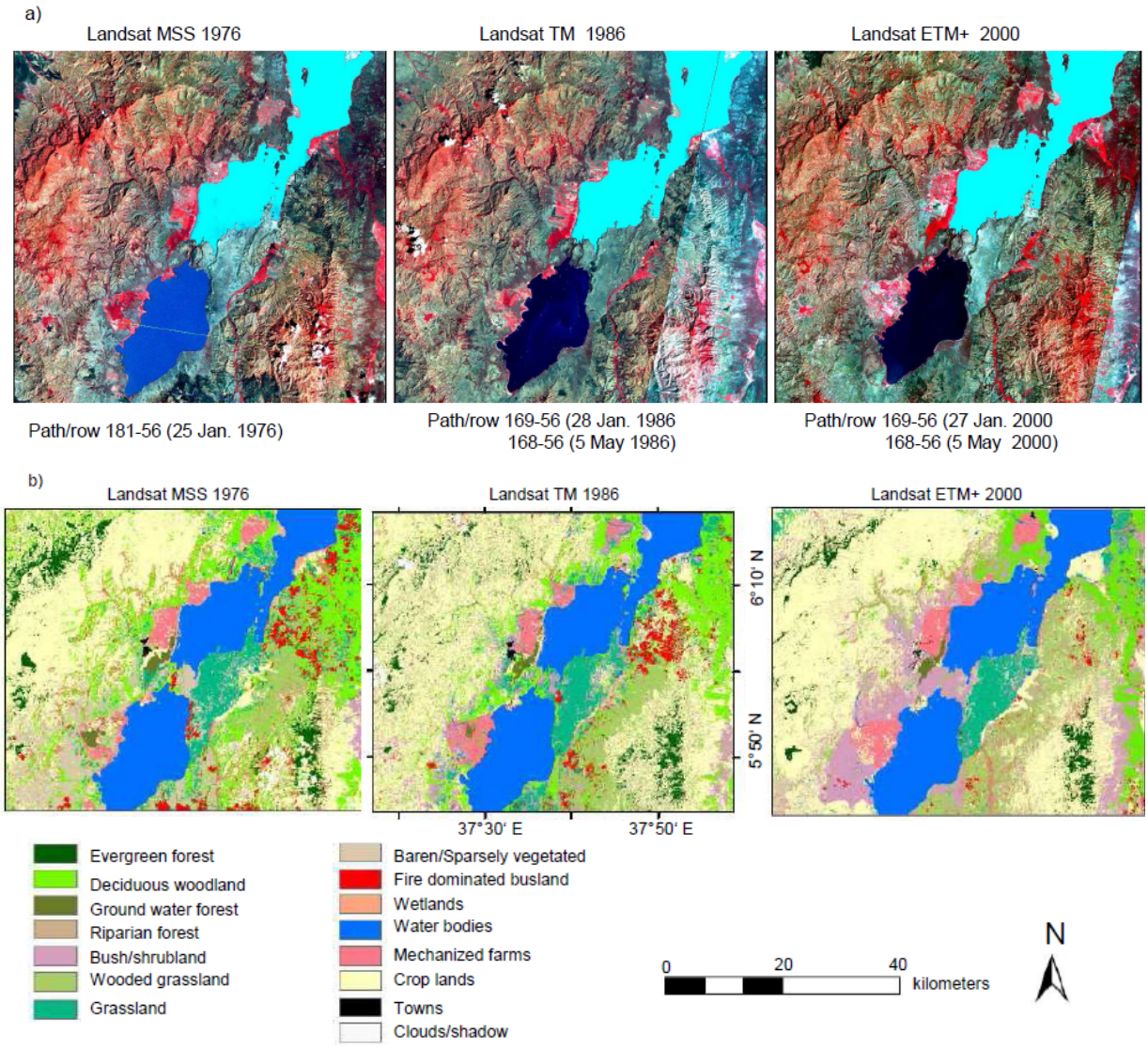

Figure 3 a) Landsat images, paths/rows and data of acquisition; b) Classified land use/land cover maps for the three time interval of 1976, 1986 and 2000.

Over the whole period of two and a half decades (1976-2000) most land cover classes conceded some of their land to croplands (Table 3). In the first decade barren/sparsely vegetated land cover and deciduous forest (woodland) lost the largest area of land to cropland, ~167 km² and ~90 km², respectively. Many of these land cover changes to cropland are because of agricultural expansion in the areas adjacent to cropland in the highlands and possibly as a result of migration to the lowlands along the Rift Valley on the western border

of Lake Chamo (Figure 2). Although agricultural conversion dominated the landscape during the first decade, it was also observed that land cover transformations took place extensively in the landscape. For instance, a significant part of the deciduous woodland was transformed into bush/shrubland, riparian forest (~76 km² each) and grassland (~60 km²). Furthermore, wooded grassland was largely transformed into bushland and open grassland (Table 3).

Table 1 Land use/land cover (LULC) descriptions

Ser.no.	LULC types	Descriptions
1	Evergreen forest	Evergreen dry and moist afromontane forest with covers more than 70 %. The dominant species include *Apodytes dimidiata* E. Mey. ex Arn., *Ilex mitis* L. Radlk, *Arundinaria alpina* K. Schum, *Syzygium guineense* (Willd.) DC, and dense plantations of *Eucalyptus globules* and *Cupressus lustanica*.
2	Deciduous woodland	Deciduous forest or woodland with a cover range up to 60 % dominated by *Combretum spp*., *Acacia spp*., *Terminalia brownii* Fresen, and *Dichrostachys cinerea* (L.) Wight & Arn.
3	Ground-water forest	Dense forest cover which is dependent on the ground water table. Dominant species are *Lepisanthes senegalensis* (Poir) Leenh, *Ficus sycomorus* L. and *Teclea nobilis* Del.
4	Riparian forest	Deciduous and evergreen forest along the banks of streams. Dominant species are *Ficus spp*. and *Acacia spp*.
5	Wooded grassland	Open evergreen and deciduous woodlands with a cover ranging from 20 to 40 %, shrubs, scattered trees and bushes. The dominant species are *Acacia spp*., *Combretum spp*., *Euclea divinorum* Hiern, and *Dodonea angustifolia* L.f.
6	Grassland	Extensive grasslands with almost homogenously dominated by grasses and sparse trees and shrubs in the Nech-sar plains and along low lying areas. The dominant grass species include *Themeda triandra* Forssk., *Hyparrhenia spp., Heteropogon contortus* and scattered tress of *Accacia mellifera*,(Vahl) Benth., and *Dichrostachys cinerea* (L) Wight & Arn.
7	Bush/shrub woodland	Includes short shrubs, thorny bushes and tufted grasses (e.g. Heteropogon contortus (L.) Roem. & Schult.) mainly used for grazing and browsing. The dominant species include Dodonea angustifolia L.f., *Acalypha fruticosa* Forssk., *Canthium pseudosetiflorum* Brid., *Acacia spp*., *Dichrostachys cinerea* (L) Wight & Arn..
8	Fire dominated bushland	Burned areas and 'fire-successional vegetation', mainly bushlands dominated by *Dodonea angustifolia* L.f, *Accacia spp*., *Canthium pseudosetiflorum* Brid.
9	Barren/sparsely vegetated	Barelands due to excessive erosion, and sedimentations and scattered *Acacia spp*., tufted grasses and other thorny species.
10	Mechanized farms	State owned farms mainly cotton and banana plantations using heavy machineries, irrigation and fertilizers
11	Cropland	Areas covered by annual and perennial crops usually by small landholders. It includes cereals such as Teff (*Eragrostis tef*,), Barley (*Hordeum vulgaris*), Maize (*Zea mays* L.) and Wheat (*Triticum Spp*.), root crops such as cassava (*Manihot esculata* Cranz,), yams (*Dioscorea abyssinica* Hochst ex Kunth, etc) and Enset (*Enset ventricosum*). It also includes agroforestry such as apple (Malus Sylvestris Miller), mango (*Mangifera indica* L.), avocado (*Persea americana* Mill) tress in their homesteads and farm yards.
12	Town	Arba Mich town & other small towns
13	Wetlands	Swampy and marshy areas mainly around Lakes Abaya and Chamo. The shoreline of Abaya and Chamo are dominated by *Typha angustifolia* (L.), and *Aeschynomene elaphroxylon* Jaub.
14	Water bodies	Lakes Abaya, Chamo and small ponds
15	Cloud/shadow	Clouds and shadow cover during image acquisitions

In the second period (1986-2000) the pattern of landscape change and transformation took a more pervasive stage. Croplands, unlike over the previous period, gained quite large areas from many classes such as deciduous, bush/shrubland, wooded grassland and sparsely vegetated (Table 3). This shows that there was an indiscriminate process of deforestation for agricultural purposes especially in the Rift Valley regions. Deciduous woodland experienced a transition to wooded grassland and bush/shrubland, whereas bush/shrubland gained a lot of area from grassland (132 km²) and wooded grassland (124 km²) over the period from 1986 to 2000.

Table 2 Land use/land cover change between 1976 and 2000.

Land use/land cover types	1976	%	1986	%	2000	%
Evergreen forest	190.1	3.4	184.6	3.3	132.0	2.4
Deciduous woodland	903.4	16.2	695.7	12.5	438.3	7.9
Riparian forest	211.6	3.8	226.7	4.1	246.5	4.4
Bush/shrubland	100.1	1.8	397.7	7.1	669.6	12.0
Wooded grassland	460.5	8.3	448.8	8.0	446.8	8.0
Grassland	326.1	5.8	363.0	6.5	229.6	4.1
Fire-dominated bushland	225.7	4.0	152.8	2.7	63.3	1.1
Cropland	1651.7	29.6	1937.8	34.7	2112.8	37.9
Barren/sparsely vegetated	538.1	9.6	178.0	3.2	268.8	4.8
Ground water forest	30.0	0.5	22.6	0.4	18.3	0.3
Wetlands	22.1	0.4	4.7	0.1	14.9	0.3
Mechanized farms	110.1	2.0	114.9	2.1	157.7	2.8
Water bodies	773.4	13.9	771.4	13.8	775.7	13.9
Town/Arba Minch	3.9	0.1	4.3	0.1	4.4	0.1
Cloud/shadow	31.6	0.6	75.2	1.3	0.0	0.0
Total	5578.0	100.0	5578.0	100.0	5578.0	100.0

The evergreen forest (remnant Afro-montane forest) experienced a decline over the stated periods, losing an area of about 16 km² and 24 km² from 1976-1986 and 1986-2000, respectively. In general, the area of cropland and bush/shrubland increased considerably during the study period. By contrast, deciduous woodland, grassland, fire-dominated bushland, wooded grassland and evergreen forest generally showed a decline over the course of twenty-four years (Figure 3b).

Table 3 Land cover/land use change matrix showing class to class changes, total gains and Losses of different classes from1976-2000 (bold texts in the diagonal indicate the amount of cover units which persists in the subsequent reference year).

Change matrix (1976-1986)	Land use/land cover types									Area (km^2)	
	Ev	DW	RF	BS	WG	GR	FB	CL	BSV	1976	Total loss
Ev	**146.3**	10.42	5.08	0.29	10.12	0.29	0.26	15.49	0.34	190.09	43.80
DW	3.1	**487.29**	76.19	75.36	25.98	58.80	47.44	89.97	1.85	903.44	416.15
RF	7.4	46.15	**52.12**	30.13	12.26	0.48	6.72	53.77	2.07	211.61	159.49
BS	0.1	5.80	3.85	**57.59**	6.48	3.92	15.57	4.78	1.45	100.10	42.51
WG	0.96	37.61	14.39	84.54	**218.52**	50.51	6.46	45.39	1.65	460.50	241.98
GR	0.17	16.92	1.84	34.57	52.70	**135.65**	8.99	14.23	1.48	326.11	190.46
FB	0.54	12.78	2.10	47.32	85.97	22.54	**26.67**	10.62	13.32	225.65	198.98
CL	0.30	0.31	0.73	1.51	6.13	34.18	27.65	**1,500.12**	9.80	1,651.71	151.59
BS	4.45	3.54	3.80	0.98	14.99	0.50	1.01	167.16	**115.17**	538.05	422.88
1986	184.59	695.70	226.71	397.73	448.80	362.98	152.80	1,937.79	177.98	**5,578.32**	2,246.86
Total gain	38.30	208.41	174.59	340.14	230.28	227.33	126.13	437.67	62.81	2.246.86	

Change Matrix (1986-2000)										Area (km^2)	
	Ev	DW	RF	BS	WG	GR	FB	CL	BSV	1986	Total loss
Ev	**124.52**	1.91	24.96	0.18	0.58	0.04	0.19	24.13	2.18	184.60	60.08
DW	0.00	**376.20**	62.20	67.96	73.00	4.72	4.46	73.27	0.82	695.69	319.49
RF	0.00	33.47	**54.63**	51.48	18.59	1.45	1.83	47.30	0.34	226.71	172.08
BS	0.00	1.13	30.93	**126.22**	72.82	30.32	5.62	77.66	14.39	397.73	271.51
WG	0.00	3.06	4.34	124.74	**180.24**	41.84	12.90	73.80	3.85	448.80	268.56
GR	0.00	1.80	0.86	132.21	33.39	**126.42**	4.74	45.50	3.44	362.99	236.57
FB	0.42	8.67	0.99	98.76	9.27	6.78	**12.56**	11.97	0.92	152.80	140.24
CL	1.00	2.96	1.40	8.38	10.86	8.98	18.23	**1,685.58**	150.41	1,937.80	252.22
BS	0.00	0.33	0.14	4.63	20.11	2.44	0.60	65.01	**80.94**	177.97	97.03
2000	132.00	438.33	246.50	669.60	446.80	229.56	63.30	2,112.80	268.84	**5,578.46**	2.010.57
Total gain	7.48	62.13	191.87	543.38	266.56	103.14	50.74	427.22	187.90	2.010.57	

EV:Tropical evergreen forest; **DW**: Deciduous woodland; **RF**: Riverine forest; **BS**: Bush/shrubland; **WG**: Wooded Grassland; **GR**: Grassland; **FB**: Fire dominated bushland; **CL**: Cropland; **BSV**: Barren/sparsely vegetated).

Discussion

Land use/land cover changes the Gughe-Amaro Highlands

In the highland of the Gughe-Amaro Mountains small-scale crop cultivation dominates the pattern of land cover change. It covers above 40 % of the study area (excluding Lakes Abaya and Chamo). Evergreen forest and deciduous forest/woodland have suffered from deforestation and degradation due to the direct conversion of forest to farmland and through logging and human settlement. In the mid 1970s the Gughe-Amaro Highlands already lost

the climax afro-montane vegetation to farmland. However, there were still some remnant patches of evergreen dry afromontane forest (1900-3200 m) and moist afromontane forest (2000-3200 m) (Desissa 2007) on higher mountain tops and on inaccessible steep slopes. This remnant forest, however, still lost area to cropland in subsequent decades. Similarly, riparian forests lost a significant area (~ 100 km^2) between 1976 and 2000 (Table 3).

A high population density in the highlands since 1970s resulted in the conversion of forests to croplands. Kloos & Adugna (1989) estimated annual population growth rate of 1.9 % for Gamo Gofa region between 1967 and 1984. Based on this growth rate and retrospective projections for our study area from 1994 census results (CSA 1996), the total population in 1976 was estimated to be 221,643 and 57,088 in the Gughe highlands (Chencha, Dita, Daramalo and Bonke sub-districts) and the Amaro highlands (Amaro special woreda/sub-district), respectively. This would yield a population density of 116 persons/km^2 and 36 persons/km2. The total rural population density has nearly doubled over the last three decades (1976-2007) with the current rural population density at 214 persons/km² and 89 persons/km² (Population Census Commission 2008) in the Gughe and Amaro highlands, respectively.

Based on the Central Statistical Agency 1996 projection, some administrative sub-districts like Chencha in the Gughe highland had a density of more than 320 persons/km² (CSA 1996). It was reported that cropland holding consistently declined from a hectare per household in 1970 to 0.25 hectare per household in 2000 in Gamo Gofa (Farina et al. 2001). This evidently had a result on the fragmentation and degradation of the mountain forest vegetations**.** The Gughe highland, in particular, faced a significant loss and degradation of the evergreen afro-montane forest. The remnants of this forest have already been fragmented with the potential consequence of biodiversity loss and regional precipitation change over time. Localized plant species extinctions, the vulnerability to invasive species, and decreased ecosystem resilience were reported to be severe in East Africa due to climate change and variability (Case 2006).

Owing to the declining man-to-land ratio and a consequent decline of local agricultural production, farming communities started to heavily depend on foreign food aid, out migration to urban centres and to the lowlands such as the nearby Rift Valley. McCann's extensive work on the Central Ethiopian highlands (Ankober) has also revealed the continual

out-migration of people from the Ankober highlands to the adjacent Rift Valley to take on agricultural lands as a consequence of the declining people-to-land ratio and environmental degradation (McCann 1995). In the same context, an out-migration of the population as a survival strategy was observed in the northern Ethiopian highlands because of poverty and environmental degradation (Ezra 2001).

Land cover dynamics in the Rift Valley

The process of LULCC in the Rift Valley section of the study area was dominated by a simultaneous process of deforestation and transformation of land us/land cover types. Much of the vegetation cover except for the evergreen afro-montane forest was concentrated in the Rift Valley section of the study area (see Figure 3b). The expansion of croplands was a pervasive process in the second reference period of the study (1986-2000), gaining quite large areas from many land cover types such as deciduous forest/woodland, bush/shrubland, wooded grassland and sparsely vegetated areas. This shows that there was an indiscriminate process of deforestation for agricultural purposes.

The transition of deciduous forest/woodland to wooded grassland and riparian forest was a conspicuous process from 1976 to 2000 (Table 3). However, the transition of deciduous forest/woodland to grassland has shown a differential rate of transformation over the two reference periods. The first reference period (1976-1986) was signified by a marked transition from deciduous forest/woodland to grassland (~59 km²). The period 1976-1986 in Ethiopia was characterized by a shift in tenure policy, villagization/resettlement and climate variability (drought) (Kloos & Adugna 1989; Ayenew 2004). The transition of deciduous forest/woodland was mainly to wooded grassland ~73 km² in the period 1986-2000 compared to 26 km² in the first reference period (1976-1986). This, therefore, is a possible indication of differential processes taking place over the two specified periods; the first study period was likely dominated by the forest clearing for cropland and thinning of the vegetation through logging for construction materials and hence encouraged the dominance of grassland. It has been reported that population growth and in-migration to the Rift Valley regions, unemployment and government policies (e.g., land tenure, resettlement, mechanized agriculture) were found to be important drivers of LULCC since 1970s in Ethiopian Rift Valley regions (Reid et al. 2000; Gessesse & Christiansson 2008). In addition in the mid 1970s the prevalence of drought, evidenced by a fall in the lake levels of Lake Abaya and

Lake Chamo (Ayenew 2004), and population displacement from the highlands (Reid et al. 2000) have resulted in the extensive transformation of the landscape in the nearby Rift Valley and its adjacent lowlands.

In the subsequent period, however, the transition of deciduous woodland to grassland was surpassed by wooded grassland. This could possibly be the result of a combination of disturbance events such as overgrazing, change in fire and the change in precipitation regimes from the late 1980s to 2000 (Ayenew 2004; Shütt et al. 2005). Laks Abaya and Chamo exhibited a steady increase in water levels reaching a maximum of about 3.5 meters for Lake Chamo in the year 2000 compared to the 1985 water level (Ayenew 2004), a possible indication of increased rainfall in the region. In the same context, bush/shrubland gained a great deal of area from grassland (132 km²) and wooded grassland (124 km²) over the period from 1986 to 2000. In addition to an increase in precipitation since the 1990s, the transformation of grassland to bush/shrubland could be the result of bush encroachment due to high grazing intensity by domestic and wild animals in and around the Nech Sar National Park. Fire-dominated bushland vegetation has also been transformed into bush/shrubland. However, it was not clear whether grass-dominated vegetation changed into bush/shrubland due to a change in the fire regime or simply due to a lack of fuel load for fire as a result of vegetation degradation.

The current operation of the Tsetse eradication project, which was aimed at controlling trypanosomiasis, would have its own negative effect on the transformation of the vegetation cover in the Rift Valley. The overall goal of such a project was to help enable farmers and pastoral communities to ensure food security through an increased number of healthy cattle and through the use of animal draught power (ESTC 2008). In the environmental impact assessment of the Tsetse control project run by the Ethiopian science and technology commission (ESTC 2008), it was stated that the effective control of the killer animal disease, Trypanosomiasis, would help to shift the high population pressure from the surrounding highlands.

The effect of such a project is yet to be seen but different sources indicated that Tsetse control projects in Africa have accelerated the conversion of woodlands and forests at the expense of agricultural expansion (Nagel 1993; Wilson et al. 1997). For instance, a study conducted by Wilson and his colleagues indicated that the effective control of Tsetse flies in

the Ghibe Valley in south-western Ethiopia resulted in the accelerated conversion of wooded grassland into cropland as smallholders penetrated into previously uncultivated lands (Wilson et al. 1997).

Conclusion

There was a significant change in the land use/land cover over the study periods from 1976-2000. Land cover change and transformations have taken differential trajectories over space and time in the study area. The highlands were dominantly characterized by land cover change where most of the cover classes changed to cropland. In contrast, the Rift Valley was dominated by a combination of land cover change and transformations with processes of forest clearing for agricultural purposes and the degradation of forests and woodlands. Temporally, in the first decade cropland expansion was mainly at the expense of deciduous woodland, sparsely vegetated and riparian forest. However, in the second study period most classes lost a significant proportion of land to agriculture and a concomitant shift from one land cover class to another due to a combination of socio-economic factors, climatic variability and possibly a shift in tenure regimes.

The consequences of LULCC (e.g., biodiversity loss, regional precipitation change) are very critical. The Gughe highland, in particular, faced a significant loss and degradation of evergreen afro-montane forest. The remnants of this forest were already fragmented and subject to the potential consequences of biodiversity loss and regional precipitation change over time. Therefore, the overall pattern and trajectories of LULCC in the study area were consequences of different factors spanning from local to regional responses to demographic, socio-economic and government policy regimes. Such changes bring about far-reaching consequences to local human livelihoods, biodiversity loss and regional environmental change.

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Diversity and Distributions, in preparation

Climate warming and tropical plant species – consequences of a potential upslope shift of isotherms in southern Ethiopia

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Abstract

Aim Species reportedly respond to global warming by poleward and altitudinal distribution shifts. We tested the following hypotheses to predict potential response of species to global warming in the tropics: 1) Consequences of global warming result in strong potential lowland attrition, range-gaps, range contractions, and finally extinction risks of plants. 2) There are growth forms and plant families which face a higher than average risk due to their current altitudinal distribution. 3) Endangered and endemic species are especially vulnerable to warming.

Location South Ethiopian highlands.

Method We applied a simple model developed by Colwell *et al.,* 2008 to evaluate the consequences of an upward shift of isotherms on the altitudinal distribution of 475 plant species in southern Ethiopia. Temperture increase between 0 and 5°C were modelled. Differences between groups of species were evaluated by a permutation procedure and GLM's.

Results Even mild global warming created strong potential risks concerning lowland attrition, i.e. the net loss of species richness in the tropical lowlands caused by altitudinal range shifts in the absence of new species arriving. Likewise, many species are projected to face range gap shifts, i.e. the absence of an overlap between future and current altitudinal ranges already at

mild warming scenarios. Altitudinal contractions and mountaintop extinctions became important only after warming exceeded 3.5°C. Area per species declined by 55% (A2 emission scenario) as a consequence of the physical shape of the mountains. Endemic species as well as herbs and ferns showed over-proportionally high vulnerability. Several plant families with higher or lower risk than average were identified.

Main conclusions Lowland biotic attrition and range shift gaps pose urgent challenges in the inner tropics, while range contractions especially threaten endemic and already endangered species. We suggest that conservation priorities can be identified with the help of the applied model even in the absence of precise regional warming scenarios.

Keywords
Climate change, tropics, lowland attrition, range-gap shifts, range contractions, extinction

Introduction

Alterations of species distributions due to global warming result in poleward and upward shifts (Beckage *et al.,* 2008; Lenoir *et al.,* 2008; Parmesan & Yohe, 2003; Pauli *et al.,* 2007) across a wide variety of taxa (Hickling *et al.* 2006). The vast majority of these observations stem, however, from the mid- to high latitudes (Felton *et al.,* 2009). This is clearly not adequate with regard to climate change scenarios, which predict stronger than average warming in the tropics (IPCC, 2007). These scenarios furthermore project both climatic conditions without current equivalents and the loss of current climatic conditions mainly in the tropics, with a hotspot of turnover in the east African mountains (Williams *et al.,* 2007). Estimated global-warming-induced rates of species extinctions in tropical biodiversity hotspots is even projected to exceed those due to land use, supporting the suggestion that global warming is one of the most serious threats to tropical biodiversity (Malcolm *et al.* 2006).

The inner tropics display a special case where the lack of a latitudinal temperature gradient makes any latitudinal shift of species distributions highly unrealistic, leaving altitudinal range shifts as the only viable solution for species migrations (Colwell *et al.,* 2008). Only a few observations support current altitudinal range shifts for the tropics (Bustarnante *et al.* 2005;

Chen *et al.,* 2009; Pounds *et al.,* 1999; Raxworthy *et al.,* 2008). The geological past, mainly the Pleistocene, provides further evidence that tropical species react to temperature changes by altitudinal range shifts (Bush, 2002; Mayle *et al.,* 2004; Umer *et al.,* 2007).

The potential magnitude for altitudinal range shifts in the tropics can be illustrated by a simple model which basically accounts for the expected warming by shifting the altitudinal range of species according to the shift of isotherms. By applying this model, Colwell *et al.,* (2008) identify four basic ecological challenges in the face of warming: lowland attrition, range-gap shifts, range contraction, and extinction. At temperate latitudes, space formerly occupied by species now shifting poleward or upslope may be occupied by species already adapted to warmer temperatures, i.e. species from lower latitudes or lower elevations. The same general pattern applies for tropical mountains, where upslope range shifts may be compensated by the influx of species from lower elevations or by expansion from small nuclei left over from previous warming episodes (Bush, 2002). But no places warmer than the tropical lowlands exist, implying that no species which currently occupy warmer habitats within dispersal reach may fill any gaps created by altitudinal shifts of species from the tropical lowlands. It can therefore be expected that tropical lowlands may experience biotic attrition, i.e. the loss of species without replacement (Colwell *et al.,* 2008). Range gaps are not only a tropical concern, as they describe the challenge of reaching suitable climatic conditions by migration when current and future suitable habitats do not overlap. Altitudinal ranges of a vast number of tropical species is narrow (Ghalambor *et al.,* 2006), a fact that implies more numerous range shift gaps in the tropics than at higher latitudes. Range contraction and extinction are finally consequences of the physical constraints by the given altitude of the summits. This phenomenon is widely discussed as “mountaintop extinction” and is a strong concern for endemic species lacking disjunct populations elsewhere on higher mountains or at cooler latitudes (Lenoir *et al.,* 2008; Williams *et al,.* 2007; Williams *et al.,* 2003).

Here, we apply the model developed by Colwell *et al*., (2008) on a dataset of altitudinal vegetation surveys in southern Ethiopia to test the following hypotheses:
1) Consequences of global warming result in strong potential lowland attrition, range-gaps, range contractions, and finally extinction risks of plant species of southern Ethiopia. 2) There are growth forms and plant families which face a higher than average risk due to their current

altitudinal distribution. 3) Endangered and endemic species are especially vulnerable to warming.

Material & Methods

Study area

The study area is located at 5°40'N to 6°37'N and 37° 12'E to 37° 59'E (Figure 1) in the southwest Ethiopian highlands. The landscape includes different physiographic features such as plateaus, escarpments, a block mountain, undulating plains, and a graben where Lake Abaya and Lake Chamo are located. The lake level displays the lowest altitudes of the region, with significantly lower areas below at least 800 m are located more than 200 km south from our study area. The topography of the Rift Valley consists of hills, as well as flat and faulted structures. The eastern boarder is marked by the Amaro horst, a block mountain that emerged during the formation of the Rift Valley. The western escarpment of the Rift Valley down from the Chencha Highlands is characterized by steep slopes and a topography that is greatly dissected by small streams, which drain into Lake Abaya and Lake Chamo.

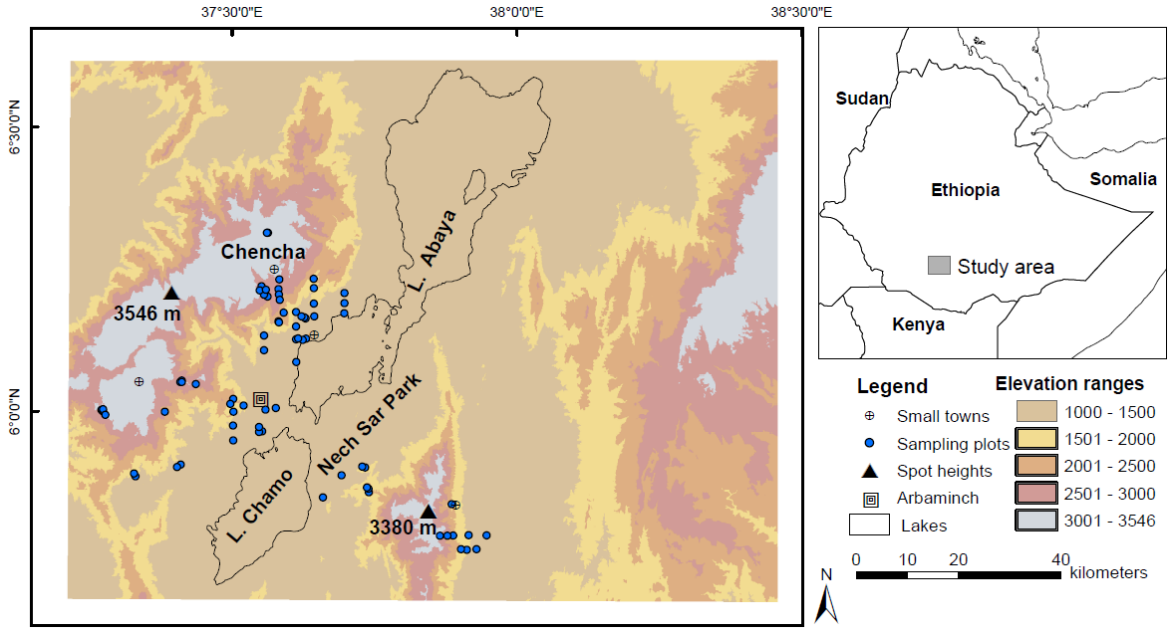

Figure 1 Digital Elevation Model (DEM) of the study area based on SRTM digital elevation data.

Rainfall in the study area shows a pronouncedly bimodal seasonal distribution. The mean annual rainfall recorded for Arbaminch (at 1200 m altitude) in the period from 1987 to 2005 was 888 mm while for Chencha (at 2700 m), for the period 1972 to 1980 and 1990 to 2004, 1235 mm were recorded (meterological data were obtained from Nationail Meterological Agency of Ethiopia). The main rainy season, which accounts for about 40 % of the mean annual rainfall, occurs from April to June, while the lesser rainy season is in September and October. Arbaminch experiences a more pronounced dry season and receives less rainfall because of its low altitude and its rain-shadow position with regard to the moisture-bearing south-east trade winds that prevail in April/May and September/October months in the region. The vegetation of the study area belongs to the Somali-masai regional center of endemism and the highlands belong to the Afromontane archipelago according to White (1983). The World Conservation International has recently identified the horn of Africa region as one of the 34 hotspots of biodiversity (Sodhi *et al.,* 2007). The Rift Valley section of our study area belongs to the arid belt of this biodiversity hotspot. The remnants of broad leaved afromontane vegetation are highly fragmented due to human settlement. The remaining relatively dense vegetation cover is found in the escarpment of the Rift Valley and in the Netch Sar National Park.

Sampling design

We aimed at a proportional sampling of the altitudinal gradient by consulting a digital elevation model (DEM) of the study area. The DEM was constructed from SRTM digital elevation data sources (Jarvis *et al.,* 2008). A roughly proportional percentage of plots were allocated to the corresponding elevation ranges with the exception of the elevation band between 1000 and 1200 m a.s.l., where the majority of the surface is covered by the two lakes. No sampling was conducted above 3000 m due to logistic problems and difficulties of access during fieldwork. For each of the 200-meter ranges (10 altitudinal ranges between 1000 and 3000 m a.s.l.), sampling was conducted depending on the presence of forest, woodland or any category of semi-natural vegetation in the landscape. Agricultural fields and plantations were not sampled.

A total of 74 plots of 400 m^2 each were sampled (see Figure 1) in two phases, from November 2006 to January 2007, and in December 2007, respectively. Both phases of fieldwork were conducted after the small rainy season. Plant species presence and growth form information

were recorded. Growth form categories included woody, herbs, graminoids and ferns. A total of 475 species belonging to 101 families were encountered during fieldwork (Appendix I). For those species that could not be identified precisely in the field, specimens were taken to the National Herbarium at the Addis Ababa University for identification or confirmation. The family Fabaceae was represented by 58 species (12.2 %), Asteraceae by 48 species (10 %), Poaceae 34 species (7.2 %), Lamiaceae and Acanthaceae by 45 species each (9.5%), Euphorbiacceae and Rubiaceae by 33 species (7 %). These seven families represented roughly 46% of the data set in the study area. More than half of the families were represented either by one species (32 families) or two species (23 families).

Estimation of current and future altitudinal ranges

Estimations of altitudinal ranges based on sampling data are always minimum estimates, especially for diverse tropical communities (Kluge *et al.,* 2006). Our sampling was not continuous along the transects, but occurred at discrete plots. Thus, the observed altitudinal range of a species detected at only one site would equal zero. All observed ranges were therefore interpolated and extrapolated by assuming continuous ranges (interpolation) from lowest to highest occurrence in the dataset and by extrapolating each observed range at both its lower and upper altitudinal limits by the range estimate downslope or upslope halfway to the nearest plot. For plots at the lowest and highest altitudes extrapolation was made halfway to Rift Valley bottom or to the summit elevation respectively (Colwell *et al.,* 2008). Both extrapolation and interpolation are conservative adjustments with regard to the principal conclusions of this study (Colwell *et al.,* 2008).

Due to the uncertainty of climate change scenarios, we analyzed the response over the range between 0°C to 5°C warming. Several analyses were based on 4.2 °C warming by 2100 compared to 2000 according to the A2 emission scenario for east Africa (IPCC, 2007). Adiabatic lapse rate in the study area is nowadays about 0.6°C per 100 m altitude (Peyron *et al.,* 2000).

We applied a simple model to evaluate the potential effects of climate warming on the distribution of species ranges on a bounded altitudinal gradient (Colwell *et al.,* 2008), which is explained in Figure 2. Altitudinal ranges were translated into area using the DEM in order to evaluate area contraction with species shifts. Differences in area contractions between

groups of species were evaluated by a permutation procedure comparing the observed mean difference of the groups with 10 000 random permutations using the function “diffmean” in the package “simba” (Jurasinski, 2007).

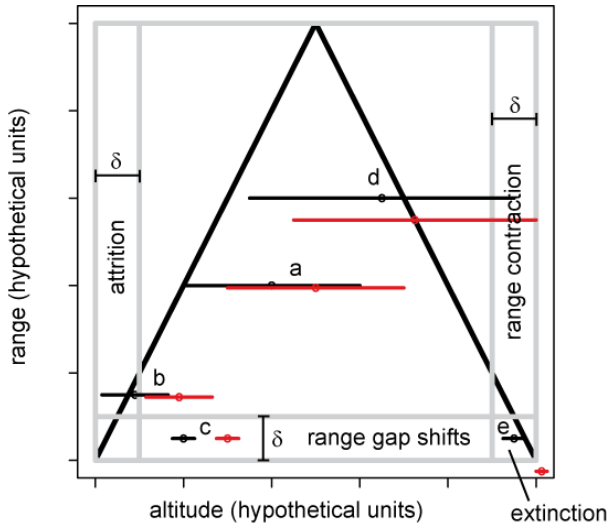

Figure 2 Graphical model illustration. The altitudinal range of each species is displayed as a function of its altitudinal midpoint, with corresponding range limits indicated by the solid horizontal lines (black: current range, red: future range). All range-size/range-midpoint coordinate pairs are within the geometric constraint triangle (black lines), as ranges cannot extend beyond the limits of the gradient. δ indicates the upslope shift in isotherms with warming climate, which is the exclusive parameter of the model. Five basic scenarios are displayed with hypothetical species: (a) An upslope shift by δ of a species with a range and altitudinal midpoint outside the grey margin boxes has no influence on the four basic challenges presented in the following four cases. (b) Lowland biotic attrition occurs for all species with a current lower range limit within minimum altitude plus δ. (c) Range-shift gaps occur for all species with a range smaller than δ resulting in no overlap of current and future range. (d) Range contractions are inevitable for all species with an upper range limit exceeding maximum altitude minus δ. (e) If species exhibit a range smaller than δ combined with an upper range limit exceeding maximum altitude minus δ the model expects mountaintop extinction.

The 1997 IUCN red list of threatened plant species (Walter & Gillet, 1998) and a recently updated red list plants of Ethiopia and Eritera (Vivero *et al.,* 2006a, b) were consulted to determine the endemic status of species. *Prunus africana* and *Hagenia abyssinica* are considered highly endangered trees in East Africa since the rate of uses exceeds far beyond the natural regenerative capacity of the two species (Feyissa *et al.,* 2005; Negash, 2004). Because of the high ecological and economic significance of these two species in Ethiopia and elsewhere in Tropical Africa, we pay special attention to them. Binomial GLM were used to evaluate if endemic and red list species differed in their potential risks concerning attrition,

range gap shifts, contraction, and extinction from all other species. If significant group effects occurred, TukeyHSD post-hoc comparisons were applied to evaluate the pairwise differences. All analyses were run in R (R Development Core Team, 2008).

Results

The 475 plant species sampled in the altitudinal transects showed a clear tendency to rather low altitudinal distributions with small ranges (Figure 3 A). This was reflected by a high proportion of species potentially contributing to lowland attrition or subject to range gap shifts already at mild to medium warming scenarios (Figure 3 B). Range contractions and extinction risks started to increase only at warming scenarios of more than 3.5°C. Area per altitude decreases with increasing altitude for our study area. Consequently, projected altitudinal range changes were expected to lead to strong area contractions (Figure 4) even with few species experiencing altitudinal range contractions. Assuming 4.2°C warming, mean area per species decreased from 892 km² to 489 km², a contraction by 55%.

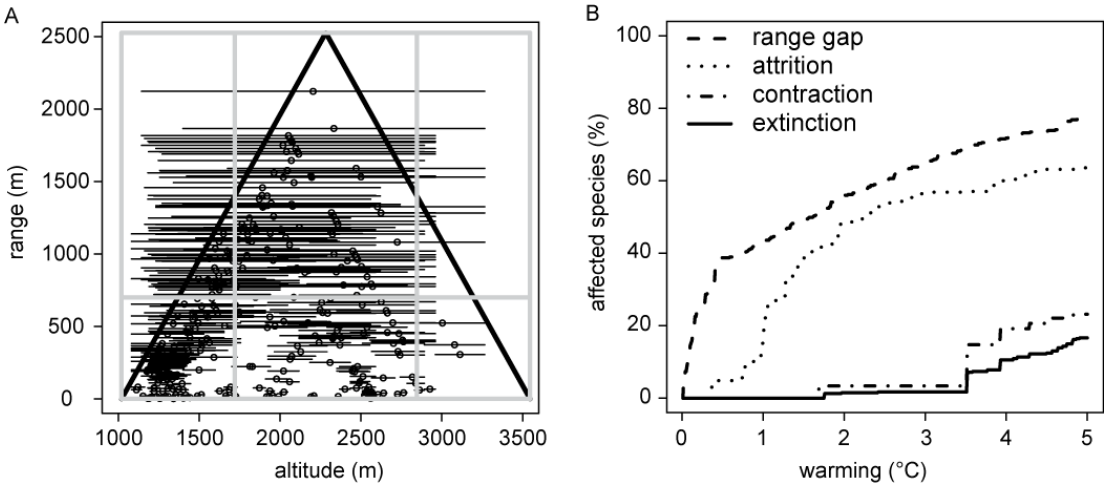

Figure 3: A: Current ranges of the 475 species. The model (Figure 2) is displayed with a warming scenario of 4.2°C, resulting in an altitudinal shift of isotherms (δ) by 700 m (grey boxes). B: Share of species subject to attrition, range gap shifts, range contractions, and extinction as a function of warming.

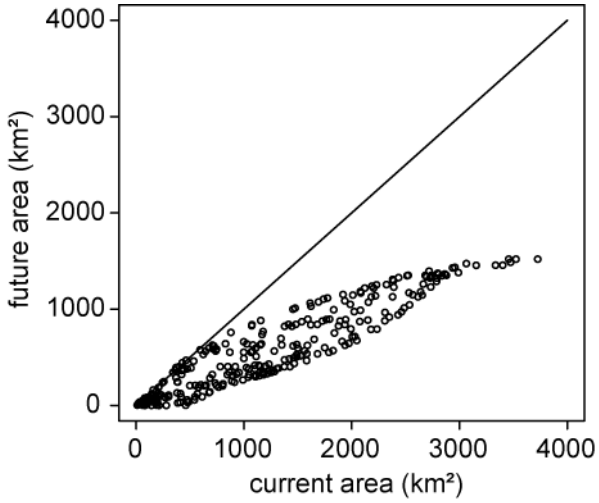

Figure 4 Area contraction per species. Current and future area was derived from a Digital Elevation Model of the current and future altitudinal range of each of the 475 species.

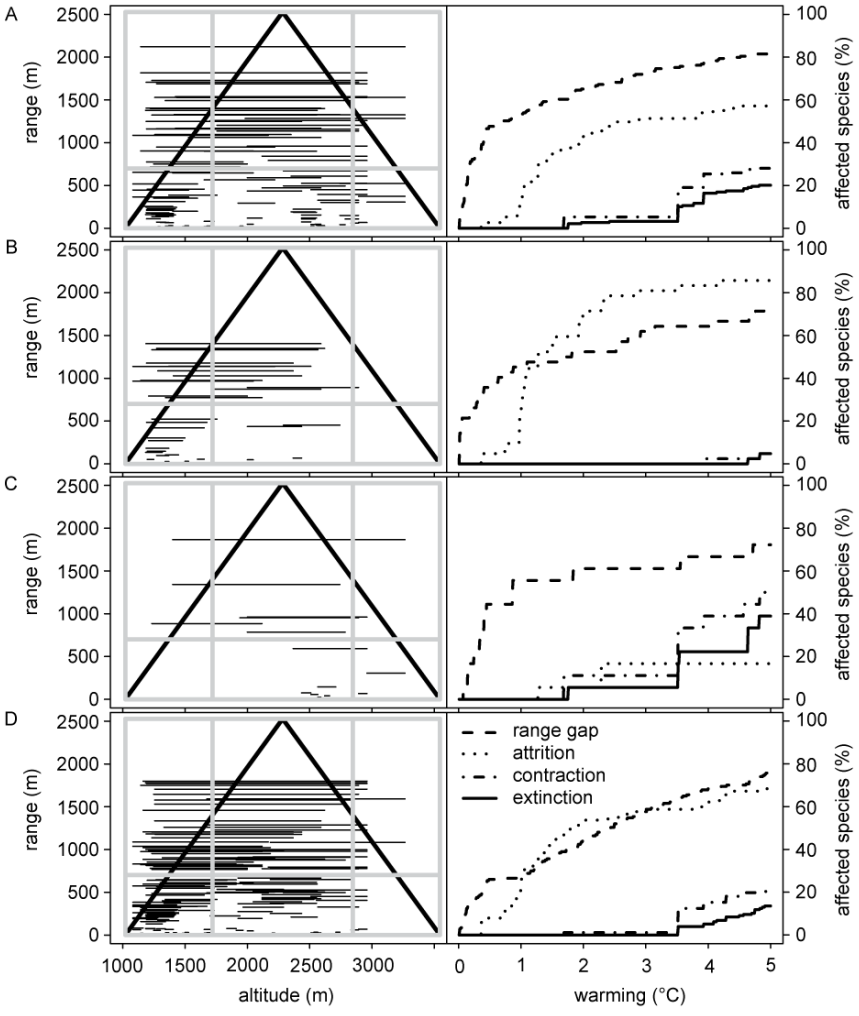

Figure 5 Current ranges and share of species subject to attrition, range gap shifts, range contractions, and extinction as a function of warming separated by growth forms. A: herbs, B: graminoids, C: ferns, D: woody species.

Growth forms differed in their response to warming according to their altitudinal distributions (Figure 5). Concerning lowland attrition (GLM: $p < 0.001$) post hoc comparisons confirmed that ferns were generally less often affected than all other groups. No significant difference concerning range shift gaps were found between the growth forms (GLM: $p = 0.085$). Altitudinal range contraction affected growth forms differently (GLM: $p < 0.001$) with less effects on graminoids than herbs and ferns (no significant difference between graminoids and woody species). Extinction risk also differed between the growth forms (GLM: $p < 0.001$), in the pair-wise comparison, however, only a higher extinction risk for herbs compared to graminoids yielded significance.

Plant families generally differed in their altitudinal distributions. Several plant families with higher as well as lower risks of area contraction than all other families could therefore be identified (Table 1). Detailed information on altitudinal range distributions and the share of species subject to attrition, range gap shifts, range contractions, and extinction as a function of warming for all 101 families can be found in the Electronic Appendix.

Table 1 Plant families which exhibit significantly (permutation procedure $p < 0.05$, analysis only run if families contained more than one species, 69 families were eligible for analysis) different area contractions per species when compared to all other species. Mean contraction per species over all 101 families was 55%.

Family	Area contraction (%)	Mean current area per species (km²)	Mean area per species with 4.2°C warming (km²)	Number of species
Thymelaeaceae	2.7	53	52	2
Pittosporaceae	2.9	425	413	2
Campanulaceae	36.2	480	306	4
Oleaceae	40.8	1601	948	4
Vitaceae	52.4	1327	631	7
Overall mean	***55.0***	***892***	***489***	***475***
Euphorbiaceae	60.2	941	375	18
Convolvulaceae	64.5	357	127	7
Polypodiaceae	91.6	56	5	2
Gentianaceae	99.5	117	1	3

24 endemic species occurred in our dataset (Table 2). These species generally showed a lower risk of contributing to lowland attrition (20.8% vs. 63.6%; GLM: $p < 0.001$), a higher potential for altitudinal range contractions (41.7% vs. 18.0%; GLM: $p < 0.001$) and extinction (33.3% vs. 10.2%; GLM: $p = 0.001$) compared to all other species at a warming scenario of 4.2°C. No significant difference in range gap shifts were found (79.2% vs. 72.7%; GLM: $p = 0.490$). Figure 6 implies that strong increases in range contraction and extinction risks started with a warming of about 3.5°C, while range gaps virtually occurred at minimum warming scenarios.

The two endangered tree species *Hagenia abyssinica* and *Prunus africana* differed in their potential response to assumed global warming. *H. abyssinica* shares the potential risk of extinction, altitudinal range contraction and range gap shift with most of the endemic species (Table 2). *P. africana*, however, exhibited potential lowland attrition and range gap contraction.

Our model predicted a significant area contraction for nine out of the 69 families which were candidates for this analysis (Table 1). These families generally exhibited a higher than average potential risk of range contraction and extinction (GLM: $p < 0.05$). The families Gentianaceae and Polypodiaceae were predicted to suffer disproportionately stronger from extinction with a decline in the potential area of over 90 % at the global warming scenario of 4.2°C temperature increase. The three most abundant families (Fabaceae, Asteraceae and Poaceae), which represented about 30 % of our species data set, did not show any significant difference to the average response to the projected global warming. Nevertheless, Fabaceae and Poaceae showed low risk of extinction and high rates of lowland attrition while Asteraceae tend to be more vulnerable to extinction and range gap shifts at global warming scenarios above 3.5°C (for details see Appendix I).

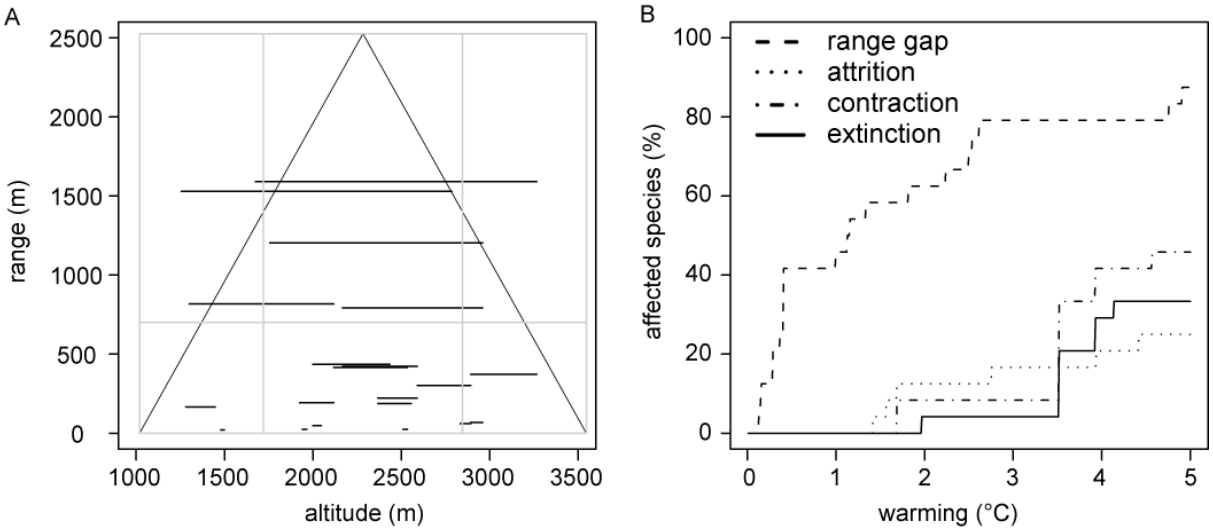

Figure 6 A: Current ranges of 24 endemic species (Table 2) and B: Share of endemic species subject to attrition, range gap shifts, range contractions, and extinction as a function of warming. All axes directly comparable to Figure 3.

Table 2 Projected consequences for endemic species at a warming of 4.2°C.

species	family	Status	current distribution			future distribution (4.2°C warming)			consequence			
			lower range limit (m)	upper range limit (m)	area (km²)	lower range limit (m)	upper range limit (m)	area (km²)	attrition	extinction	contraction	range gap
Bothriocline schimperi	Asteraceae	LC	1256	2785	2682	1956	3485	1351	1	0	0	0
Crassocephalum macropappum	Asteraceae	LC	2368	2590	232	3068	3290	110	0	0	0	1
Crotalaria agatiflora subsp. enlangeri	Fabaceae	NT	2893	3266	280	3546	3546	0	0	1	1	1
Crotalaria gillettii	Fabaceae	endemic	1479	1499	84	2179	2199	31	1	0	0	1
Dorestenia soerensenii	Moraceae	VU	2510	2534	44	3210	3234	17	0	0	0	1
Emilia herbaceae	Asteraceae	endemic	2000	2047	79	2700	2747	77	0	0	0	1
Emilia serpentinus	Asteraceae	endemic	2368	2555	200	3068	3255	101	0	0	0	1
Erythrina brucei	Fabaceae	LC	2118	2534	421	2818	3234	363	0	0	0	1
Euphorbia dumalis	Euphorbiaceae	LC	2893	2960	79	3546	3546	0	0	1	1	1
Justicia bizuneshiae	Acanthaceae	endemic	1940	1965	57	2640	2665	50	0	0	0	1
Kalanchoe petitiana	Crassulaceae	LC	1756	2960	1445	2456	3546	822	0	0	1	0
Kniphofia isoetifolia	Asphodilaceae	endemic	2833	2893	82	3533	3546	0	0	1	1	1
Leucus abyssinica	Lamiaceae	LC	1301	2118	1764	2001	2818	891	1	0	0	0
Lippia adoensis	Verbenaceae	LC	1675	3266	1794	2375	3546	897	1	0	1	0
Pimpinella schimperi	Apiaceae	endemic	2000	2435	464	2700	3135	468	0	0	0	1
Pittosporum abyssinica	Pittosporaceae	endemic	1925	2118	257	2625	2818	248	0	0	0	1
Plectocephalus varians	Asteraceae	endemic	2893	2960	79	3546	3546	0	0	1	1	1
Pycnostachys abyssinicus	Lamiaceae	endemic	2168	2590	422	2868	3290	321	0	0	0	1
Satureja paradoxa	Lamiaceae	NT	2590	2893	387	3290	3546	0	0	1	1	1
Senecio myriocephalus	Asteraceae	LC	2893	2960	79	3546	3546	0	0	1	1	1
Thunbergia annua	Acanthaceae	endemic	2000	2047	79	2700	2747	77	0	0	0	1
Urtica simensis	Urticaceae	endemic	2168	2960	866	2868	3546	0	0	1	1	0
Verbasum benthamianum	Scrophulariaceae	endemic	2893	2960	79	3546	3546	0	0	1	1	1
Hagenia abyssinica	Rosaceae	endangered*	2893	2960	79	3546	3546	0	0	1	1	1
Prunus africana	Rosaceae	endangered*	1163	2960	3474	1863	3546	1488	1	0	1	0

*not endemic but of high economic importance, see text for details, LC = Less Concern, NT = Near Threatened, VU = Vulnerable species (IUCN categories).

Discussion

Even moderate global warming caused strong potential risks concerning lowland attrition and range gap shifts, while altitudinal contractions and mountaintop extinctions became important only after warming exceeded 3.5°C in our dataset from southern Ethiopia. Area per species, however, was expected to decline by 55% on average even in the absence of strong altitudinal range contractions. This pattern was due to the physical shape of the mountains.
Existing reports of observed upward shifts in the tropics are available only for a small number of animal groups (Bustarnante *et al.,* 2005; Chen *et al.,* 2009; Pounds *et al.,* 1999; Raxworthy *et al.,* 2008). We are not aware of any such an observation concerning plants, even though plants act as ecosystem engineers by providing the micro-habitat for the fauna and are therefore of high ecological relevance.

Lowland biotic attrition, i.e. the net loss of species richness in the tropical lowlands caused by upslope range shifts in the absence of new species arriving, depends on the assumption that tropical lowland species are already living at their thermal optimum. From the geological past, Colwell *et al.* (2008) conclude that "many lowland tropical species may be in for trouble if they do not shift to higher elevations or to cooler, wetter microhabitats in coming decades". For our study region, past climate change resulted in fast and strong altitudinal range shifts (Umer *et al.,* 2007). The idea of lowland attrition is further supported by experimental studies indicating that tropical ectotherms are already living at temperatures near their thermal optimum and show declines in fitness with further warming (Deutsch *et al.,* 2008). Likewise, growth decline of lowland tropical trees has been related to increasing temperatures (Clark *et al.,* 2003; Feeley *et al.,* 2007). Tropical lowlands therefore will likely experience decreased species richness, with novel plant communities composed of heat and drought tolerant or early successional species (Williams *et al.,* 2007).

Range gaps are no exclusive tropical concern, as they pose the challenge of reaching suitable climatic conditions by migration when current and future suitable habitats do not overlap. Tropical species, however, may face range shift gaps more often than temperate species because of the generally narrow altitudinal ranges of a vast number of tropical species (Ghalambor *et al.,* 2006). Climatic factors have always changed in mountainous zones and species have responded by range shifts; the extent and degree of alteration by global warming is the core of current concern (Young & Lipton, 2006). The main question regarding range

gaps in particular and altitudinal migration in general is the potential dispersal distance, which is poorly studied, especially for tropical plant species (Weir & Corlett, 2007). Genetic diversity patterns of a species restricted to several mountains in east Africa nevertheless imply that occasional long-distance dispersal events occur even between mountains (Ehrich *et al.,* 2007). Species facing range-shift gaps will furthermore have to compete with wide-ranged species that continue to occupy upslope portions of their current ranges (Bush *et al.* 2004), even though range retractions at the warm end of species distributions seem to keep pace with range extension at the cold end (Franco *et al.,* 2006; Raxworthy *et al.,* 2008; Wilson *et al.,* 2007). Inertia in the response of the whole system nevertheless limits potential upward shift (Adams, 2007; Jentsch & Beierkuhnlein, 2003).

Range contraction and extinction are general consequences of reduced area per altitude towards mountain summits. This phenomenon is widely discussed as "mountaintop extinction" and is a strong concern for endemic species lacking disjunct populations elsewhere on higher mountains or at cooler latitudes (Lenoir *et al.,* 2008; Williams *et al.,* 2007; Williams *et al.,* 2003). Endangered and endemic species appear especially vulnerable in our dataset due to their restricted range and their tendency to occur at mid to high altitudes, which seems to be a general pattern for endemic species (Erasmus *et al.,* 2002; Ohlemuller *et al.,* 2008; Raxworthy *et al.,* 2008). Extinction of formerly endemic mountaintop species accompanied by succeeding, mostly widely distributed, species from lower elevations may lead furthermore to the loss of beta-diversity on the landscape level (Jurasinski & Kreyling, 2007).

Concerning the growth forms, ferns appeared more susceptible than the other groups in our study, a pattern that is related to their generally high-altitudinal distribution. This fact differs from findings in cloud-forest transects (Kluge *et al.,* 2006), implying that differences in vulnerability between growth forms are regionally dissimilar. Unlike observations in the temperate zone (Lenoir *et al.,* 2008), graminoids, in our dataset, show the least response in terms of contraction and extinction risks due to their low altitudinal distribution.
Patterns of plant families' response generally resembled the responses of their growth forms. Thus, the most affected families were largely represented by herbs and ferns (e.g Gentianaceae and Polypodiaceae). Those families which were found to be abundant in our data set showed more resilience to extinction and range contraction compared to others. However, the potential response of high lowland attrition and subsequent depauperation of

species belonging to the two economically and ecologically important families such as Fabaceae and Poaceae may have adverse consequences in the lowlands under global warming. Though species are generally expected to be sifted out depending on their ability to migrate or in situ persist (Midgley *et al.,* 2007), the loss of constituent species from the aforementioned families might result in the loss of vital ecological services such as nitrogen fixation and important range resources in the low lying semi-arid ecosystems of the tropics.

The two endangered tree species, *Hagenia abyssinica* and *Prunus africana* have shown a differential response to global warming scenarios within our study area. The potential response of *H. abyssinica* to global warming showed a high risk of extinction, range contraction and range gap shifts while *P. africana* was found to be potentially subject to lowland attrition and affected by range contraction. The response of *H. abyssinica* is particularly due to its tendency to occur at high altitude. It may have once been the dominant tree species in the upper montane forest belt, but now is only found as scattered trees in the highlands (Feyissa *et al.,* 2005; Hedberg & Edwards, 1989). The response of *P. africana* to lowland attrition was probably due to its occurrence around Arbaminch forest, which is sustained by high ground water table along the shores of Lakes Abaya and Chamo. Apart from their differential response to potential consequences of global warming, these two species share common characteristics of being limited to mountainous regions of tropical Africa and hence considered as Afromontane endemic and Afromontane near endemic, respectively (Friis, 1992). Both species, and probably several others with similar status (e.g. *Olea europaea* subsp. *cuspidata*), appear strongly affected by the combined effect of global change and their excessive use beyond their regenerative capacities.

Our results describe worst-case scenarios, even if warming occurs as assumed, mainly because of the method to determine altitudinal range limits. The estimation based on our sampling very likely underestimates regional altitudinal range (Miller *et al.* 2007). Comparably to climate envelope models (Pearson & Dawson, 2003), we assume furthermore that the fundamental climatic niche of each species is fully expressed by current distributions; that the effects of climate outweigh any idiosyncratic effects of species interactions, dispersal limitation, demographic patterns, or historical contingency; and that habitats at the landscape scale are homogenous with regard to microclimate. Species that currently occupy warmer microhabitats at their lower range limit may for instance also shift to currently cooler refuges

at the same elevation during warming (Bush, 2002; Bush *et al.,* 2004). Even fast genetic adaptation may be possible (Ozgul *et al.,* 2009).

On the other hand, our simple model solely based on temperature does not take factors into account which may exacerbate the projected consequences. In the lowlands, decreased precipitation and increased fire frequency may amplify the direct effects of increased temperature, as plants depend on future changes in precipitation as well as in temperature because temperature and precipitation interact strongly through transpirational water loss (Tilahun, 2006). Climate change is furthermore expected to reduce cloud formation at higher altitudes and hence increase the rate of evapotranspiration from tropical montane forests (Sodhi *et al.,* 2007). The horn of Africa, particularly Ethiopia, has already experienced increased incidences of drought and rainfall variability owing to the combined effects of regional atmospheric circulation patterns and sea surface temperature anomalies (Bewket & Conway, 2007; Segele *et al.,* 2009).

Anthropogenic habitat fragmentation and widespread interruption of altitudinal corridors pose strong general concern on the potential of species migrations. The current reserves, which are believed to host the majority of biodiversity in Ethiopia, are surrounded by anthropogenically transformed and fragmented landscapes (Edwards & Westoby, 1996). Any natural migration out of these reserves appears therefore questionable. The Nech Sar National Park, which is located along the eastern shores of Lakes Abaya and Chamo, is the only park in Ethiopia with a relatively viable status (Jones, 2005). However, population increases in the adjacent highlands and in Arbaminch town, permanent settlement within the park and subsequent pressure of intense grazing and land use change have already started to fragment the park's ecosystem (Jones, 2005). Our model furthermore projects strong lowland attrition for this park, as it is located at the regionally lowest altitude. The general pattern with a high species richness at the lowest altitude might partly by caused by the National Park. The relatively low human disturbance at the lowest altitudes could generally be due to the fact that the lowlands were infested by Malaria and Trypanomiases (cattle disease) and hence were avoided from early human settlement.

Adaptation policies in Ethiopia focus on agricultural production with shifting management strategies and changing target crops (Bryan *et al.,* 2009), but it seems also likely that the zone of agriculture will move upslope faster than the natural species and therefore landscape

conversion might contradict the ability of some species to access suitable habitat (Bush, 2002). Biotic interactions are another cause for concern, as idiosyncratic responses may disrupt current interactions (Bush, 2002; Parmesan, 2006). Range-shift projections focus furthermore on immediate consequences, ignoring long-term effects of decreased suitable habitat and smaller populations, where land area declines with increasing elevation (Jentsch & Beierkuhnlein, 2003).

Conclusions

Global warming must be expected to pose strong threats on tropical diversity. Biotic lowland attrition is emerging as an urgent challenge exclusive to the inner tropics. It basically depends on the question if lowland species can physiologically tolerate warmer (and drier) conditions than they experience today. This can be answered by experiments. The high share of species at risk of range shift gaps demands detailed exploration of potential natural dispersal and, as a final step, consideration of assisted colonization especially in highly fragmented landscapes. In addition, current reserve management such as Nech Sar National Park and future reserve design should take into account the potential impact of global warming to curb the loss of species via creating species migration corridors. Families and species of high concern can be identified with the applied model based on their current distribution without the need of precise local warming predictions. Special conservation attention is necessary regarding endemic and summit species, which generally show a strong vulnerability. Here, exploration of the total geographical range and potential maximum elevation limits will be needed, although ex-situ conservation may be the only option for many of these species.

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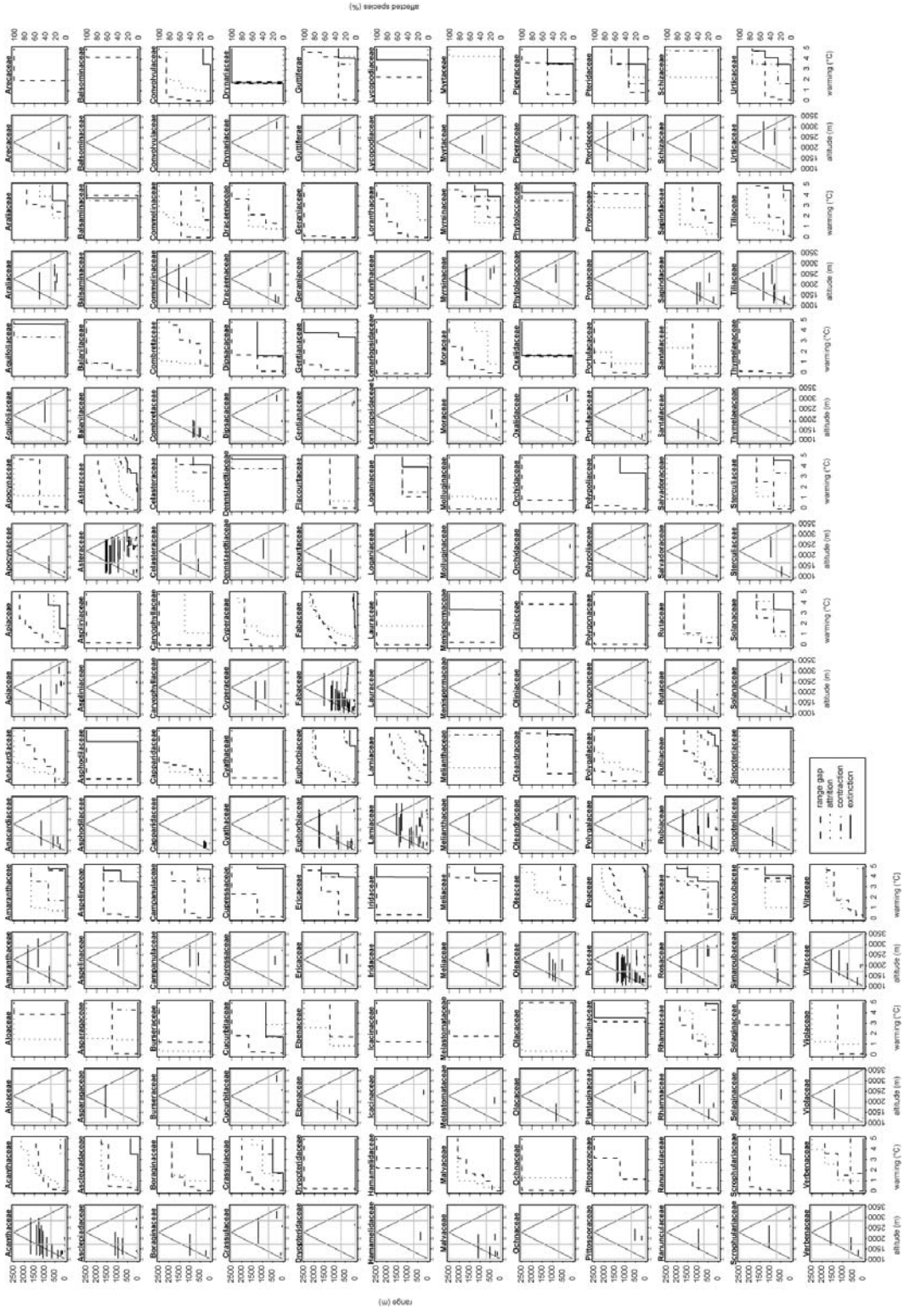
Electronic Appendix for Manuscript 4

I. Current ranges and share of species subject to attrition, range gap shifts, range contractions, and extinction as a function of warming for all 101 families (see Figure 3 on MS 4 for details).



Electronic Apendix for Manuscript 4

II. Species, Families and Growth forms of 475 plant species encountered in the field

Nomenclature follows the published Flora volumes of Ethiopian and Eritrea (Edwards *et al.* 1995, 1997, 2000; Hedberg & Edwards 1989, 1995; Hedberg *et al.* 2003, 2004)

Abrevations: He = Herbs, Wo = Woody, Cl = Climbers, Gr = Graminoids, Fe = Ferns

Species	Families	Growth forms
Acanthus eminens C.B.Clarke	Acanthaceae	Wo
Barleria eranthemoides R. Br. ex C.B.Clarke	Acanthaceae	He
Barleria grandicalyx Lindau	Acanthaceae	He
Barleria ventricosa Hochst. ex Nees.	Acanthaceae	He
Blepharis maderaspatensis (L.) Roth	Acanthaceae	He
Crabbea velutina S. Moore	Acanthaceae	He
Dicliptera maculata Nees	Acanthaceae	He
Hypoestes forskaolii (Vahl) R. Br.	Acanthaceae	He
Hypoestes triflora (Forssk.) Roem. & Schult.	Acanthaceae	He
Isoglossa punctata (Vahl) Brumitt & Wood.	Acanthaceae	He
Isoglossa sp.	Acanthaceae	He
Justicia bizuneshiae Ensermu	Acanthaceae	He
Justicia cordata (Nees) T. Anderson	Acanthaceae	He
Justicia flava (Vahl) Vahl	Acanthaceae	He
Justicia glabra Koenig ex Roxb.	Acanthaceae	He
Monechma debile (Forssk.) Nees	Acanthaceae	He
Phaulopsis imbricata (Forssk.) Sweet	Acanthaceae	He
Ruellia patula Jacq.	Acanthaceae	He
Ruellia prostrata Poir.	Acanthaceae	He
Thunbergia alata Boj. ex. Sims	Acanthaceae	Cl
Thunbergia annua Hoshst.	Acanthaceae	Cl
Aloe sp.	Aloaceae	Wo
Achyranthes aspera L.	Amaranthaceae	He
Cyathula cylindrica Moq.	Amaranthaceae	He
Pupalia grandiflora Peter	Amaranthaceae	He
Lannea triphylla (A. Rich.) Engl.	Anacardiaceae	Wo
Ozoroa insignis Del.	Anacardiaceae	Wo
Rhus natalensis Krauss	Anacardiaceae	Wo
Rhus ruspolii Engl.	Anacardiaceae	Wo
Sclerocarya birrea (A. Rich.) Hochst.	Anacardiaceae	Wo
Agrocharis melanantha Hochst.	Apiaceae	He
Alepidea peduncularis Stued. ex A. Rich.	Apiaceae	He
Centella asiatica (L.) Urban	Apiaceae	He
Heracleum abyssinicum (Boiss.) Norman	Apiaceae	He
Heteromorpha arborescens (Spreng.) Cham. & Schlecht.	Apiaceae	Wo
Pimpinella oreophila Hook. f.	Apiaceae	He
Pimpinella schimperi Abebe	Apiaceae	He
Sanicula elata Buch.-Ham.ex D. Don	Apiaceae	He
Torilis arvensis (Hudson) Link	Apiaceae	He
Acokanthera schimperi (A.DC.) Schweinf.	Apocynaceae	Wo
Carissa spinarum L.	Apocynaceae	Wo
Ilex mitis (L.) Radlk.	Aquifoliaceae	Wo

Species	Families	Growth forms
Schefflera myriantha (Bak.) Drake	Araliaceae	Wo
Phoenix reclinata Jacq.	Arecaceae	Wo
Dregea abyssinica (Hochst.) K. Schum.	Asclepiadaceae	Cl
Edithcolea grandis N. E. Br.	Asclepiadaceae	He
Gomphocarpus fruticosus (L.) Ait. f.	Asclepiadaceae	He
Periploca linearifolia Quert.-Dill. & A. Rich.	Asclepiadaceae	Cl
Sarcostemma viminale (L.) R. Br.	Asclepiadaceae	Cl
Secamone parvifolia (Oliv.) Bullock	Asclepiadaceae	Cl
Tacazzea conferta N. E. Br.	Asclepiadaceae	Cl
Asparagus africanus Lam.	Asparagaceae	Cl
Asparagus flagellaries (Kunth) Baker	Asparagaceae	Cl
Kniphofia isoetifolia Steud. ex. Hochst.	Asphodelaceae	He
Asplenium aethiopicum (Burm. f.) Bech.	Aspleniaceae	Fe
Asplenium anisophyllum Kze.	Aspleniaceae	Fe
Asplenium erectum Willd	Aspleniaceae	Fe
Asplenium monanthes L.	Aspleniaceae	Fe
Adenostemma mauritianum DC.	Asteraceae	He
Ageratum conyzoides L.	Asteraceae	He
Aspilia africana (Pers.) C.D. Adams	Asteraceae	He
Aspilia mossambicensis (Oliv.) Wild	Asteraceae	He
Bidens pachyloma (Oliv. & Hiern) Cufod.	Asteraceae	He
Bidens pilosa L.	Asteraceae	He
Bidens ternata (Chiov.) Sherff	Asteraceae	He
Blumea caffra (DC.) O. Hoffm.	Asteraceae	He
Bothriocline schimperi Oliv. & Hiern ex Benth.	Asteraceae	He
Carduus leptacanthus Fresen.	Asteraceae	He
Conyza newii Oliv. & Hiern	Asteraceae	Wo
Conyza pedunculata (Oliv.) Wild.	Asteraceae	He
Conyza pyrrhopappa Sch.Bip. ex A. Rich.	Asteraceae	Wo
Conyza sumatrensis (Retz.) E.H. Walker	Asteraceae	He
Crassocephalum macropappum (Sch. Bip. ex A. Rich.) S. Moore	Asteraceae	He
Crepis rueppellii Sch. Bip.	Asteraceae	He
Dichrocephala integrifolia (L.f.) Kuntze	Asteraceae	He
Eclipta prostrata (L.) L.	Asteraceae	He
Emilia herbaceae Mesfin & Beentje	Asteraceae	He
Emilia serpentines Mesfin & Beentje	Asteraceae	He
Guizotia schimperi Sch. Bip. ex Walp	Asteraceae	He
Helichrysum argyranthum O.Hoffm.	Asteraceae	He
Helichrysum foetidum (L.) Moench.	Asteraceae	He
Helichrysum formosissimum Sch. Bip. ex A. Rich.	Asteraceae	He
Helichrysum globosum A. Rich.	Asteraceae	He
Helichrysum nudifolium (L.) Less.	Asteraceae	He
Helichrysum schimperi (Sch. Bip ex A.Rich.) Moeser	Asteraceae	He
Helichrysum traversii Chiov.	Asteraceae	He
Inula paniculata (Klatt) Burtt-Dary	Asteraceae	He
Kleinia squarrosa Cufod.	Asteraceae	Wo
Laggera crispata (Vahl) Hepper & Wood	Asteraceae	He
Melanthera scandens (Schumach. & Thonn.) Roberty	Asteraceae	Cl
Microglossa pyrifolia (Lam.) Kuntze	Asteraceae	Wo
Parthenium hysterophorus L.	Asteraceae	He
Plectocephalus varians (A. Rich.) C. Jeffrey ex. Cufod.	Asteraceae	He
Pluchea dioscoridis (L.) DC.	Asteraceae	He
Senecio hadiensis Forssk.	Asteraceae	He
Senecio myriocephalus Sch. Bip. ex A. Rich.	Asteraceae	Wo
Senecio subsessilis Oliv. & Hiern	Asteraceae	He
Sonchus oleraceus L.	Asteraceae	He

Species	Families	Growth forms
Vernonia auriculifera Hiern.	Asteraceae	Wo
Vernonia galamensis (Cass.) Less.	Asteraceae	He
Vernonia hymenolepis A. Rich.	Asteraceae	Wo
Vernonia myriantha Hook. f.	Asteraceae	Wo
Vernonia popeana C. Jeffrey	Asteraceae	He
Vernonia urticifolia A. Rich.	Asteraceae	Wo
Vernonia wollastonii S. Moore	Asteraceae	He
Xanthium strumarium L.	Asteraceae	He
Balanites aegyptiaca (L.) Del.	Balanitaceae	Wo
Balanites rotindifolia (van Tieghem) Blatter	Balanitaceae	Wo
Impatiens hochstetteri Warb.	Balsaminaceae	He
Impatiens tinctoria A. Rich.	Balsaminaceae	He
Cordia africana Lam.	Boraginaceae	Wo
Cordia ovalis R.Br.	Boraginaceae	Wo
Cynoglossum amplifolium Hochst. ex A. DC.	Boraginaceae	He
Ehertia cymosa Thonn.	Boraginaceae	Wo
Commiphora habessinica (Berg) Engl.	Burseraceae	Wo
Lobelia gibberoa Hemsl.	Campanulaceae	Wo
Monopsis stellarioides (Presl.) Urb.	Campanulaceae	He
Wahlenbergia erectum (Roth. ex Roem. & Schult.) Tuyn	Campanulaceae	He
Wahlenbergia hirsuta (Edgew.) Tuyn	Campanulaceae	He
Boscia salicifolia Oliv.	Capparidaceae	Wo
Cadaba farinosa Forssk.	Capparidaceae	Wo
Capparis fascicularis DC.	Capparidaceae	Cl
Crateva adansonii DC.	Capparidaceae	Wo
Maerua crassifolia Forssk.	Capparidaceae	Wo
Cerastium octandrum A. Rich.	Caryophyllaceae	He
Polycarpaea eriantha Hochst.	Caryophyllaceae	He
Maytenus arbutifolia (A. Rich.) Wilczek	Celastraceae	Wo
Maytenus gracilipes (Welw. ex Oliv.) Exell	Celastraceae	Wo
Maytenus senegalensis (Lam.) Exell	Celastraceae	Wo
Combretum aculeatum Vent.	Combretaceae	Wo
Combretum collinum Fresen.	Combretaceae	Wo
Combretum molle R. Br. ex G. Don	Combretaceae	Wo
Terminalia brownii Fresen.	Combretaceae	Wo
Terminalia schimperiana Hochst.	Combretaceae	Wo
Aneilema rendlei C.B. Clarke	Commelinaceae	He
Commelina africana L.	Commelinaceae	He
Commelina benghalensis L.	Commelinaceae	He
Commelina diffusa Burm.f.	Commelinaceae	He
Commelina reptans Brenan	Commelinaceae	He
Cyanotis barbata D. Don	Commelinaceae	He
Cyanotis foecunda Hochst. ex. Hassk.	Commelinaceae	He
Convolvulus kilimandschari Engl.	Convolvulaceae	Cl
Evolvulus alsinoides (L.) L.	Convolvulaceae	He
Ipomoea cairica (L.) Sweet	Convolvulaceae	Cl
Ipomoea heterotricha F. Didr.	Convolvulaceae	He
Ipomoea kituiensis Vtake	Convolvulaceae	Cl
Ipomoea obscura (L.) Ker-Gawl.	Convolvulaceae	Cl
Seddera arabica (Forssk.) Choisy	Convolvulaceae	He
Crassula alsinoides (Hook.f.) Engl.	Crassulaceae	He
Kalanchoe glaucescens Britten	Crassulaceae	He
Kalanchoe lanceolata (Forssk.) Pers.	Crassulaceae	He
Kalanchoe petitiana A. Rich.	Crassulaceae	He
Umbilicus botryoides A. Rich.	Crassulaceae	He
Kedrostis foetidissima (Jacq.) Cogn.	Cucurbitaceae	Cl

Species	Families	Growth forms
Lagenaria abyssinica (Hook.f.) C. Jeffrey	Cucurbitaceae	Cl
Zeheneria scabra (Linn. f.) Sond.	Cucurbitaceae	Cl
Cupressus lusitanica Miller	Cupressaceae	Wo
Juniperus procera Hochst. Ex Endl.	Cupressaceae	Wo
Cyathea sp.	Cyatheaceae	Fe
Carex chlorosaccus C.B. Clarke	Cyperaceae	Gr
Carex johnstonii Böckl.	Cyperaceae	Gr
Cyperus alopecuroides Rottb.	Cyperaceae	Gr
Cyperus dubius Rottb.	Cyperaceae	Gr
Cyperus alternifolius L	Cyperaceae	Gr
Cyperus papyrus L.	Cyperaceae	Gr
Cyperus sesquiflorus (Torr.) Mattf. & Kük.	Cyperaceae	Gr
Schoenoplectus corymbosus (Roem. & Schult.) Rayn	Cyperaceae	Gr
Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae	Fe
Dipsacus pinnatifidus Steud. ex A. Rich.	Dipsacaceae	He
Pterocephalus frutescens Hochst. ex A. Rich.	Dipsacaceae	He
Dracaena afromontana Mildbr.	Dracaenaceae	Wo
Sansevieria ehrenberii Schweinf. ex Baker	Dracaenaceae	He
Sansevieria forskoaliana (Shult. f.) Heper & Wood.	Dracaenaceae	He
Drynaria volkensii Hiern.	Drynariaceae	Fe
Polystichum fuscopaleaceum Alston	Dryopteridaceae	Fe
Polystichum transvaalense C.N. Anthony	Dryopteridaceae	Fe
Diospyros abyssinica (Hiern) F. White	Ebenaceae	Wo
Euclea divinorum Hiern	Ebenaceae	Wo
Agarista salicifolia (Comm. ex Lam.) Hook.f.	Ericaceae	Wo
Erica arborea L.	Ericaceae	Wo
Erica tenuipilosa (Engl. ex Alm & Fries) Cheek	Ericaceae	Wo
Acalyha fruticosa Forssk.	Euphorbiaceae	He
Acalypha crenata A. Rich.	Euphorbiaceae	Wo
Acalypha villicaulis A. Rich.	Euphorbiaceae	Wo
Acalypha volkensii Pax	Euphorbiaceae	He
Clutia abyssinica Jaub. & Spach.	Euphorbiaceae	Wo
Croton macrostachyus Del.	Euphorbiaceae	Wo
Euphorbia ampliphylla Pax	Euphorbiaceae	Wo
Euphorbia borenensis A. Gilbert	Euphorbiaceae	Wo
Euphorbia dumalis S.Carter	Euphorbiaceae	Wo
Euphorbia inaequilatera Sond.	Euphorbiaceae	He
Euphorbia polyacantha Pax	Euphorbiaceae	Wo
Euphorbia schimperiana Scheele	Euphorbiaceae	He
Euphorbia sp. 1	Euphorbiaceae	Wo
Euphorbia sp. 2	Euphorbiaceae	Wo
Euphorbia tirucalli L.	Euphorbiaceae	Wo
Flueggea virosa (Willd.) Voigt.	Euphorbiaceae	Wo
Phyllanthus maderaspatensis L.	Euphorbiaceae	Wo
Ricinus communis L.	Euphorbiaceae	He
Acacia albida Del.	Fabaceae	Wo
Acacia brevispica Harms	Fabaceae	Wo
Acacia hockii De Wild.	Fabaceae	Wo
Acacia mellifera (Vahl) Benth.	Fabaceae	Wo
Acacia nilotica (L.) Willd. ex Del.	Fabaceae	Wo
Acacia polyacantha Willd.	Fabaceae	Wo
Acacia senegal (L.) Willd.	Fabaceae	Wo
Acacia seyal Del.	Fabaceae	Wo
Acacia tortilis (Forssk.) Hayne	Fabaceae	Wo
Aeschynomene abyssinica (A. Rich.) Vatke	Fabaceae	Wo
Aeschynomene elaphroxylon Jaub.	Fabaceae	Wo

Species	Families	Growth forms
Albizia gummifera (J.F.Gmel.) C.A.Sm.	Fabaceae	Wo
Albizia schimperiana Oliv.	Fabaceae	Wo
Alysicarpus rugosus (Willd.) DC.	Fabaceae	He
Calpurnia aurea (Ait.) Benth.	Fabaceae	Wo
Chamaecrista mimosoides (L.) Greene	Fabaceae	He
Clitoria ternatea L.	Fabaceae	Cl
Crotalaria agatiflora Schweinf. subsp.enlangeri Bak.f.	Fabaceae	He
Crotalaria cephalotes Steud. A. Rich.	Fabaceae	He
Crotalaria cylindrica A. Rich.	Fabaceae	He
Crotalaria gillettii Polhill	Fabaceae	He
Crotalaria laburnifolia L.	Fabaceae	He
Desmodium adscendens (Sw.) DC.	Fabaceae	He
Desmodium barbatum (L.) Benth.	Fabaceae	He
Desmodium repandum (Vahl) DC.	Fabaceae	Cl
Desmodium velutinum (Willd.) DC.	Fabaceae	Wo
Dichrostachys cinerea (L.) Wight & Arn.	Fabaceae	Wo
Dolichos sericeus E. Mey.	Fabaceae	Cl
Entada abyssinica Steud. ex A. Rich.	Fabaceae	Wo
Eriosema robustum Bak.	Fabaceae	Cl
Erythrina brucei Schweinf.	Fabaceae	Wo
Glycine wightii (Wight & Arn.) Verdc.	Fabaceae	Cl
Indigofera amorphoides Jaub. & Spach	Fabaceae	He
Indigofera arrecta Hochst ex A. Rich.	Fabaceae	Wo
Indigofera atriceps Hook. F.	Fabaceae	Wo
Indigofera brevicalyx Bak.f.	Fabaceae	He
Indigofera colutea (Burm.f.) Merr.	Fabaceae	He
Indigofera emarginella Steud. ex A. Rich.	Fabaceae	Wo
Indigofera garckeana Vatke	Fabaceae	Wo
Indigofera spicata Forssk.	Fabaceae	He
Macrotyloma axillare (E. Mey.) Verdc.	Fabaceae	Cl
Parochaetus communis D. Don	Fabaceae	He
Piliostigma thonningii (Schumach.) Milne-Redh.	Fabaceae	Wo
Pterolobium stellatum (Forssk.) Brenan	Fabaceae	Wo
Rhynchosia densiflora (Roth) DC.	Fabaceae	Cl
Rhynchosia minima (L.) DC.	Fabaceae	Cl
Rhynchosia resinosa (Hochst. ex A. Rich.) Bak.	Fabaceae	Cl
Senna obtusifolia (L.) Irwin & Barneby	Fabaceae	Wo
Sesbania sesban (L.) Merr.	Fabaceae	Wo
Tephrosia elata Deflers	Fabaceae	Wo
Tephrosia emeroides A. Rich.	Fabaceae	Wo
Tephrosia interrupta Hochst. & Steud. ex Engl.	Fabaceae	Wo
Tephrosia linearis (Willd.) Pers.	Fabaceae	Wo
Tephrosia pentaphylla (Roxb.) G. Don	Fabaceae	Wo
Tephrosia villosa (L.) Pers.	Fabaceae	Wo
Trifolium simense Fresen.	Fabaceae	He
Vigna membranacea A. Rich.	Fabaceae	Cl
Vigna parkeri Bak.	Fabaceae	Cl
Dovyalis abyssinica (A. Rich) Warb.	Flacourtiaceae	Wo
Flacourtia indica (Burm.f.) Merr.	Flacourtiaceae	Wo
Sebaea brachyphylla Griseb.	Gentianaceae	He
Swertia abyssinica Hochst.	Gentianaceae	He
Swertia lugardae Bullock	Gentianaceae	He
Geranium sp.	Geraniaceae	He
Pelargonium glechomoides Hochst.	Geraniaceae	He
Apodytes dimidiata E. Mey. ex Arn.	Icacinaceae	Wo
Hypericum quartinianum A. Rich.	Hypericaceae	Wo

Species	Families	Growth forms
Hypericum revolutum Vahl	Hypericaceae	Wo
Trichocladus ellipticus Eckl. & Zeyh.	Hamamelidaceae	Wo
Aristea abyssinica Pax	Iridaceae	He
Achyrospermum schimperi (Hochst. ex Briq.) Perkins	Lamiaceae	He
Ajuga integrifolia Buch.-Ham. ex D.Don	Lamiaceae	He
Becium filamentosum (Forssk.) Chiov.	Lamiaceae	He
Clerodendron myricoides (Hochst.) R. Br.ex Vatke.	Lamiaceae	Wo
Hoslundia opposita Vahl	Lamiaceae	Wo
Leonotis ocymifolia (Burm.f.) Iwarsson	Lamiaceae	He
Leucas glabrata (Vahl) R.Br.	Lamiaceae	He
Leucas martinicensis (Jacq.) R. Br.	Lamiaceae	He
Leucaus abyssinica (Benth.) Briq.	Lamiaceae	Wo
Ocimum lamiifolium (Hochst. ex Bent.) DC.	Lamiaceae	He
Platostoma rotundifolium (Briq.) A.J. Paton	Lamiaceae	He
Plectranthus barbatus Andr.	Lamiaceae	He
Plectranthus cylindraceus Hochst. ex Benth.	Lamiaceae	He
Plectranthus lanuginosus (Hochst. ex. Benth.) Agnew	Lamiaceae	He
Plectranthus minutiflorus Ryding	Lamiaceae	He
Plectranthus rupestris (Hochst.) Baker	Lamiaceae	He
Premna schimperi Engl.	Lamiaceae	Wo
*Pycnostachys abyssinic*a Fresen.	Lamiaceae	He
Pycnostachys eminii Gürke	Lamiaceae	Wo
Pycnostachys meyeri Gürke	Lamiaceae	Wo
Satureja abyssinica (Benth.) Briq.	Lamiaceae	He
Satureja paradoxa (Vatke) Engl.	Lamiaceae	He
Satureja pseudosimensis Brenan	Lamiaceae	He
Satureja punctata (Benth.) Briq.	Lamiaceae	He
Stachys aculeolata Hook. f.	Lamiaceae	He
Cassytha filiformis L.	Lauraceae	Cl
Buddleja polystachya Fresen.	Buddlejaceae	Wo
Nuxia congesta R.Br. ex Fresen.	Buddlejaceae	Wo
Englerina woodfordioides (Schweinf.) M. Gilbert	Loranthaceae	Wo
Erianthemum dregei (Eckl. & Zeyh.) Tieghem	Loranthaceae	Wo
Oncocalyx glabratus (Engl.) M. Gilbert	Loranthaceae	Wo
Tapianthus globiferus (A. Rich.) Tieghem	Loranthaceae	Wo
Tapianthus heteromorphus (A. Rich.)	Loranthaceae	Wo
Huperzia dacrydioides (Baker) Pic. Serm.	Lycopodiaceae	Epiphyte
Abutilon bidentatum (Hochst.) A. Rich.	Malvaceae	He
Abutilon fruticosum Guill. & Perr.	Malvaceae	He
Hibiscus machranthus Hochst. ex A. Rich.	Malvaceae	Wo
Hibiscus micranthus L.f.	Malvaceae	Wo
Kosteletzkya adoensis (Hochst. ex. A. Rich.) Mast.	Malvaceae	He
Sida ovata Forssk.	Malvaceae	He
Dissotis senegambiensis (Guill. & Perr.) Triana	Melastomataceae	He
Eckebergia capensis Saprrm.	Meliaceae	Wo
Lepidotrichilia volkensii (Gürke) Leroy	Meliaceae	Wo
Bersama abyssinica Fresen.	Melianthaceae	Wo
Stephania abyssinica (Dillion ex A. Rich.) Walp.	Menispermaceae	Cl
Corbichonia decumbens (Forssk.) Exell	Molluginaceae	He
Mollugo nudicaulis Lam.	Molluginaceae	He
Dorestenia soerensenii Friis	Moraceae	He
Ficus sur Forssk.	Moraceae	Wo
Ficus sycomorus L.	Moraceae	Wo
Ficus vasta Forssk.	Moraceae	Wo
Embelia schimperi Vatke	Myrsinaceae	Wo
Maesa lanceolata Forssk.	Myrsinaceae	Wo

Species	Families	Growth forms
Myrsine africana L.	Myrsinaceae	Wo
Myrsine melanophloeos (L.) R. Br.	Myrsinaceae	Wo
Syzygium guineense (Willd.) DC. ssp. afromontanum F. White	Myrtaceae	Wo
Ochna insermis (Forssk.) Schweinf. ex Penzig	Ochnaceae	Wo
Ximenia americana L.	Olacaceae	Wo
Jasminum abyssinicum Hochst. ex DC.	Oleaceae	Cl
Jasminum grandiflorum L.	Oleaceae	Cl
Olea europea L. ssp. cuspidata (Wall. ex G. Don) Cif.	Oleaceae	Wo
Schrebera alata (Hochst.) Welw.	Oleaceae	Wo
Arthropteris monocarpa (Cordem.) C. Chr.	Oleandraceae	Fe
Arthropteris orientalis (J.F.Gmel.) Posth.	Oleandraceae	Fe
Olinia rochetiana A. Juss.	Oliniaceae	Wo
Diaphananthe schimperiana (A. Rich.) Summerh.	Orchidaceae	He
Oxalis corniculata L.	Oxalidaceae	He
Phytolacca dodecandra L´Herit.	Phytolaccaceae	He
Peperomia abyssinica Miq.	Piperaceae	He
Piper capense L.f.	Piperaceae	He
Pittosporum abyssinica Del.	Pittosporaceae	Wo
Pittosporum viridiflorum Sims	Pittosporaceae	Wo
Plantago palmata Hook. F.	Plantaginaceae	He
Andropogon abyssinicus Fresen.	Poaceae	Gr
Aristida adscensionis L.	Poaceae	Gr
Arthraxon micans (Nees) Hochst.	Poaceae	Gr
Arundinaria alpina K. Schum.	Poaceae	Gr
Bothriochloa insculpta (Hochst. ex A. Rich.) A. Camus	Poaceae	Gr
Brachiaria leersioides (Hochst.) Stapf	Poaceae	Gr
Brachiaria serrata (Thunb.) Stapf	Poaceae	Gr
Cenchrus ciliaris L.	Poaceae	Gr
Chrysopogon plumulosus Hochst.	Poaceae	Gr
Cynodon dactylon (L.) Pers.	Poaceae	Gr
Digitaria velutina (Forssk.) P. Beauv.	Poaceae	Gr
Echinochloa pyramidalis (Lam.) Hitchc. & Chase	Poaceae	Gr
Enteropogon machrostachyus Hochst. ex A. Rich. Benth.	Poaceae	Gr
Eragrostis cilianensis (All.) Vign. ex Janchen	Poaceae	Gr
Exotheca abyssinica (Hochst ex A. Rich.) Anderss.	Poaceae	Gr
Harpachne schimperi Hochst. ex A. Rich	Poaceae	Gr
Heteropogon contortus (L.) Roem. & Schult.	Poaceae	Gr
Hyparrhenia filipendula (Hochst.) Stapf	Poaceae	Gr
Hyparrhenia hirta (L.) Stapf	Poaceae	Gr
Leptochloa obtusiflora Hochst.	Poaceae	Gr
Loudetia arundinacea (Hochst. ex A. Rich) Steud.	Poaceae	Gr
Melinus repens (Willd.) Zizka	Poaceae	Gr
Oplismenus undulatifolius (Ard.) Roem. & Schult.	Poaceae	Gr
Panicum atrosanquineum A. Rich.	Poaceae	Gr
Panicum coloratum L.	Poaceae	Gr
Panicum hochstetteri Stued.	Poaceae	Gr
Panicum maximum Jacq.	Poaceae	Gr
Panicum subalbidum Kunth	Poaceae	Gr
Perotis patens Gand.	Poaceae	Gr
Setaria incrassata (Hochst.) Hack.	Poaceae	Gr
Setaria pumila (Poir.) Roem. & Schult.	Poaceae	Gr
Setaria verticillata (L.) P. Beauv.	Poaceae	Gr
Sporoboulus piliferus (Trin.) Kunth	Poaceae	Gr
Themeda triandra Forssk.	Poaceae	Gr
Polygala albida Schinz	Polygalaceae	He

Species	Families	Growth forms
Polygala arenaria Willd.	Polygalaceae	He
Polygala erioptera DC.	Polygalaceae	He
Polygala rupicola A. Rich.	Polygalaceae	He
Polygala sadebeckiana Gürke	Polygalaceae	He
Polygala sphenoptera Fresen.	Polygalaceae	He
Polygonum afromontanium Greenway	Polygonaceae	Cl
Loxogramme lanceolata (Sw.) S. Presl.	Polypodiaceae	Fe
Pleopeltis macrocarpa (Bory ex. Willd) Kaulf	Polypodiaceae	Fe
Portulaca oleraceae L.	Portulacaceae	He
Portulaca quadrifida L.	Portulacaceae	He
Talinum portulacifolium (Forssk.) Achers. ex Schweinf.	Portulacaceae	He
Faurea speciosa Welw.	Proteaceae	Wo
Adiantum sp.	Pteridaceae	Fe
Pteris catoptera Kze.	Pteridaceae	Fe
Pteris cretica L.	Pteridaceae	Fe
Clematis simensis Fresen.	Ranunculaceae	Cl
Thalictrum rhynchocarpum Dill. & A. Rich.	Ranunculaceae	He
Helinus mystacinus (Ait.) E. Mey. ex Steud.	Rhamnaceae	Cl
Rhamnus prinoides L`Herit.	Rhamnaceae	Wo
Rhamnus staddo A. Rich.	Rhamnaceae	Wo
Ziziphus mucronata Willd.	Rhamnaceae	Wo
Alchemilla fischeri Engl.	Rosaceae	He
Hagenia abyssinica (Bruce) J.F. Gmel.	Rosaceae	Wo
Prunus africana (Hook.f.) Kalkm.	Rosaceae	Wo
Rubus apetalus Poir.	Rosaceae	Cl
Rubus steudneri Schweinf.	Rosaceae	Cl
Anthospermum herbaceum L.f.	Rubiaceae	He
Canthium oligocarpum Hiern	Rubiaceae	Wo
Canthium pseudosetiflorum Bridson	Rubiaceae	Wo
Galiniera saxifrage (Hochst.) Bridson	Rubiaceae	Wo
Galium simense Fresen.	Rubiaceae	He
Galium thunbergianum Eckl. & Zeyh.	Rubiaceae	He
Gardenia ternifolia Schumach. & Thonn.	Rubiaceae	Wo
Oldenlandia monanthos (A. Rich.) Hiern	Rubiaceae	He
Pavetta oliveriana Hiern	Rubiaceae	Wo
Pentanisia ouranogyne S. Moore	Rubiaceae	He
Pentas lanceolata (Forssk.) Deflers	Rubiaceae	He
Pentas schimperana (A. Rich.) Vtake	Rubiaceae	Wo
Psychotria orophila Petit	Rubiaceae	Wo
Psydrax parviflora (Afz.) Bridson	Rubiaceae	Wo
Psydrax schimperiana (A. Rich.) Bridson	Rubiaceae	Wo
Clausena anisata (Willd.) Benth.	Rutaceae	Wo
Teclea nobilis Del.	Rutaceae	Wo
Zanthoxylum chalybeum Engl.	Rutaceae	Wo
Dobera glabra (Forssk.) Poir.	Salvadoraceae	Wo
Salvadora persica L.	Salvadoraceae	Wo
Osyridocarpus schimperanus (A. Rich.) A. DC.	Santalaceae	Cl
Osyris quadripartita Decn.	Santalaceae	Wo
Allophyllus abyssinicus (Hochst.) Radlkofer	Sapindaceae	Wo
Dodonae angustifolia L.f.	Sapindaceae	Wo
Lepisanthes senegalensis (Juss. ex Poir.) Leenh.	Sapindaceae	Wo
Pappea capensis Eckl. & Zeyh.	Sapindaceae	Wo
Anemia schimperiana Presl	Schizaeaceae	Fe
Alectra sessiliflora (Vahl) Kuntze	Scrophulariaceae	He
Craterostigma pumilum Hochst.	Scrophulariaceae	He
Cycnium erectum Randle	Scrophulariaceae	He

Species	Families	Growth forms
Verbascum benthamianum Hepper	scrophulariaceae	He
Veronica abyssinica Fresen.	Scrophulariaceae	He
Selaginella abyssinica Spring	Selaginaceae	Fe
Brucea antidysenterica J.F. Mill.	Simaroubaceae	Wo
Harrisonia abyssinica Oliv.	Simaroubaceae	Wo
Pellaea viridis (Forssk.) Prantl.	Sinopteriaceae	Fe
Discopodium penninervium Hochst.	Solanaceae	Wo
Solanum anguivi Lam.	Solanaceae	Wo
Solanum incanum L.	Solanaceae	Wo
Dombya torrida (J.F. Gmel.) P. Bamps	Sterculiaceae	Wo
Hermannia tigreensis Hochst. ex A. Rich.	Sterculiaceae	He
Melhania velutina Forssk.	Sterculiaceae	He
Gnidia involucrata Steud. ex A. Rich.	Thymelaeaceae	Wo
Gnidia latifolia (Oliv.) Gilg	Thymelaeaceae	Wo
Corchorus trilocularis L.	Tiliaceae	He
Grewia bicolor Juss.	Tiliaceae	Wo
Grewia velutina (Forssk.) Vahl	Tiliaceae	Wo
Grewia villosa Willd.	Tiliaceae	Wo
Triumfetta brachyceras K. Schum.	Tiliaceae	Wo
Triumfetta pilosa Roth	Tiliaceae	Cl
Triumfetta tomentosa Boj.	Tiliaceae	Wo
Pilea rivularis Wedd.	Urticaceae	He
Pilea tetraphylla (Steudel) Blume	Urticaceae	He
Urerea hypselodendron (A. Rich.) Wedd.	Urticaceae	Cl
Urtica simensis Steudel	Urticaceae	He
Lantana viburnoides (Forssk.) Vahl	Verbenaceae	Wo
Lippia adoensis Hochst. ex Walp.	Verbenaceae	Wo
Phyla nodiflora (L.) Greene	Verbenaceae	He
Hybanthus enneaspermus (L.) F. Muell.	Violaceae	He
Viola abyssinica Oliv.	Violaceae	He
Cissus quadrangularis L.	Vitaceae	Cl
Cissus rotundifolia (Forssk.) Vahl	Vitaceae	Cl
Cyphostemma adenocaule (Stued. ex A. Rich.) Desc.oings ex Wild & R.B. Drumm.ond.	Vitaceae	Cl
Cyphostemma cyphoetalum (Fresen.) Desc. ex Wild & R.B. Drumm.Descoings ex Wild & Drummond	Vitaceae	Cl
Cyphostemma rivae (Gilg) Desc.oings	Vitaceae	Cl
Rhoicissus revoilii Planch.	Vitaceae	Cl
Rhoicissus tridentata (L. f.) Wild & R.B. Drumm.Willd & Drummond	Vitaceae	Cl

List of Publications*

1. Desalegn Wana & Carl Beierkuhnlein, submitted. Plant species and growth form richness along altitudinal gradients in southwest Ethiopian highlands. ***Journal of Vegetation Science***.
2. Desalegn Wana & Carl Beierkuhnlein, resubmitted. The relative abundance of plant functional types along environmental gradient in southwest Ethiopian highlands. ***Journal of Tropical Ecology.***
3. Desalegn Wana, Giriraj Amarnath & Carl Beierkuhnlein, in prep, Land use change in the southwest Ethiopian highlands. ***Journal of Mountain Research and Development***.
4. Juergen Kreyling, Desalegn Wana & Carl Beierkuhnlein, in prep. Climate warming on tropical plant species – consequences of a potential upward shift of isotherms in southern Ethiopia. ***Diversity & Distributions***
5. Desalegn Wana, 2008. Local People's perceptions and attitudes towards the management of Nech-Sar National park, Ethiopia, in: Jeffery, M., Firestone, J., and Bubna-Litic, K. (eds.) *Biodiversity conservation, Law and Livelihoods: Bridging the north-south divide*, Pp. 233-250, Cambridge University Press, New York.
6. Desalegn Wana & Zerihun Woldu, 2005. The vegetation of Chencha highlands in south Ethiopia. ***SINET: Ethiopian Journal of Science, 28: 109 -118***.
7. Desalegn Wana, 2004. Strategies for sustainable management of Nech-sar National Park, A research report submitted to Organization for Social Sciences Research in Eastern and Southern Africa (OSSREA).

* Publications listed from 1-4 were part of this thesis.

Declaration/Erklärung

Hiermit erkläre ich an Eides statt,

dass ich die vorliegende Dissertationsschrift selbständig und ohne fremde Hilfe verfasst, andere als die angegebenen Quellen und Hilfsmittel nicht benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Hiermit erkläre ich an Eides statt,

dass ich weder die vorliegende noch eine gleichartige Doktorprüfung an einer anderen Hochschule endgültig nicht bestanden habe.

(Desalegn Wana Dalacho) 27. October 2009